The Skull of *Erlicosaurus andrewsi,* a Late Cretaceus "Segnosaur" (Theropoda: Therizinosauridae) from Mongolia[1]

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ABSTRACT

The holotype of *Erlicosaurus andrewsi* Perle, 1981, from Late Cretaceous strata at Baynshin Tsav, South Gobi Aimak, Mongolia, includes an exceptionally well-preserved, nearly complete skull and mandible. *Erlicosaurus andrewsi* previously was considered a member of Segnosauria Barsbold and Perle, 1980, but recent work confirms that *Therizinosaurus cheloniformis* Maleev, 1954, is a member of this group; because Therizinosauridae Maleev, 1954, has priority, it is the valid name for the group. The holotype of *Erlicosaurus an-*

drewsi includes the only well-preserved skull presently known for any taxon of Therizinosauridae. We present a detailed redescription of this skull, emphasizing those features bearing evidence of its affinities with particular dinosaur groups. Cranial features of *Erlicosaurus andrewsi* are consistent with the hypothesis that the Therizinosauridae are members of Theropoda, and of the theropod taxon Maniraptora (as modified to include Ornithomimosauria) in particular. The skull of *Erlicosaurus andrewsi,* furthermore, shares several derived fea-

tures with Ornithomimosauria, Oviraptorosauria, and Troodontidae. We review previous hypotheses of relationship for Therizinosauridae—with Ornithischia and Prosauropoda—and find them to be based upon weak evidence.

INTRODUCTION

Beginning with the first publications on segnosaurs (Segnosauridae Perle, 1979; Segnosauria Barsbold and Perle, 1980), the unusual mixture of features in these fossils has baffled paleontologists investigating their relationships. Most striking is the combination of an opisthopubic pelvis similar to that of dromaeosaurid and avialian theropods with a hind foot that is not modified into the tridactyl pes typical of all theropods, and with cheeks and a beak as in ornithischian dinosaurs.

Hypotheses of relationships for Segnosauria, consequently, have involved both major clades of dinosaurs and both clades of Saurischia. In his description of the first known segnosaur material, Perle (1979) suggested that their affinities are with Theropoda, as did Barsbold (1979, 1983). Furthermore, Perle (1982) considered the equally enigmatic theropod *Therizinosaurus cheloniformis* Maleev, 1954, to be related to the segnosaurs. Paul (1984) hypothesized segnosaurs to be "relics [sic] of the prosauropod-ornithischian transition," whereas relationships with Sauropodomorpha were posited by Gauthier (1986) and Sereno (1989). These diverse hypotheses are reflected in the decision by the authors of the most recent review of segnosaurs to consider them "Saurischia *sedis mutabilis*" (Barsbold and Maryanska, 1990: 415).

An important contribution to resolving the problem of segnosaur relationships is the discovery of a new, primitive segnosaur relative, *Alxasaurus elesitaiensis* Russell and Dong, 1993. These authors hypothesized that *A. elesitaiensis* is the sister taxon of a group comprising *Therizinosaurus cheloniformis* and Segnosauria, and that this group together is the sister group of Troodontidae and Oviraptorosauria. Because the precise relationships between *Therizinosaurus cheloniformis* and the four genera of segnosaurs remain unclear, and because the family Therizinosauridae Maleev, 1954, has priority over the taxa Segnosauridae and Segnosauria (as well as

Enigmosauridae Barsbold and Perle, in Barsbold, 1983), the taxonomic validity of the latter two taxa is now ambiguous (e.g., the name could be applied validly at the subfamilial level). Russell and Dong (1993) proposed that the taxa formerly placed in the Segnosauria now be placed with *Therizinosaurus cheloniformis* in the Therizinosauridae, and that *Alxasaurus elesitaiensis* be placed with that family in the Therizinosauroidea. (Russell and Dong also proposed the monotypic family Alxasauridae, but we find such redundant taxa to be unnecessary; see De Queiroz and Gauthier, 1990.) We have not yet examined the specimens of *Alxasaurus elesitaiensis,* but the character evidence mustered by Russell and Dong, summarized in the following classification, is persuasive:

Therizinosauroidea (Maleev, 1954)
    Alxasaurus elesitaiensis Russell and Dong, 1993
    Therizinosauridae Maleev, 1954
        Erlicosaurus andrewsi Perle, 1981
        Segnosaurus galbinensis Perle, 1979
        Therizinosaurus cheloniformis Maleev, 1954
        Enigmosaurus mongoliensis Barsbold and Perle, 1983
        Nanshiungosaurus brevispinus Dong, 1979
        Chilantaisaurus zheziangensis Dong, 1979

Fossil remains of Therizinosauroidea are rare, and only a single skull is described for any of the six named taxa (Barsbold and Maryanska, 1990; Russell and Dong, 1993). Fortunately this skull, part of the holotype of *Erlicosaurus andrewsi,* is exquisitely preserved and nearly complete. Although it was described in detail and figured by Perle (1981) and Barsbold (1983), the unavailability of translations of these papers has limited their accessibility to paleontologists unfamiliar with Russian.

An opportunity to prepare a revised de-

scription of the skull of *Erlicosaurus andrewsi* was afforded by the visit of Perle to the American Museum of Natural History from October 1992 to January 1993, as part of the Mongolian Academy of Sciences–American Museum of Natural History Paleontological Project. The skull and mandible were photographed and videotaped, and Scanning Electron Micrographs were taken of a mandibular tooth.

Our study of this specimen and comparison with other dinosaurs supports the relationship with theropods originally suggested by Perle (1979). Furthermore, several features of the skull corroborate the affinities of Therizinosauroidae within Maniraptora hypothesized by Russell and Dong (1993). We defer a more detailed treatment of the phylogenetic relationships of Therizinosauroidea to a later date pending examination of a broader diversity of Maniraptora.

Abbreviations

AMNH American Museum of Natural History, Vertebrate Paleontology.
MAE Collections of the joint Mongolian Academy of Sciences–American Museum of Natural History Paleontological Expeditions. These specimens will eventually be deposited in the collections of the Mongolian Academy of Sciences.
PST Paleontological and Stratigraphic Section of the Geological Institute, Mongolian Academy of Sciences.

SYSTEMATIC PALEONTOLOGY

Erlicosaurus andrewsi Perle, 1981

HOLOTYPE: PST 100/111, a nearly complete skull and mandible, several fragmentary cervical vertebrae, an articulated right pes, missing the proximal ends of two of the four metatarsals, and the left humerus.

TYPE LOCALITY, GEOLOGICAL OCCURRENCE, AND AGE: The holotype of *Erlicosaurus andrewsi* is from a highly fossiliferous quarry at Baynshin (also spelled Bayshin or Bainshin) Tsav in the South Gobi (Omnogov) Aimak, Mongolia. This quarry produced a diverse vertebrate fauna from sediments considered to belong to the upper part of the Baynshirenskaya Svita (Tsybin and Kurzanov, 1979; Shuvalov and Chkikvadze, 1979). Currie and Eberth (1993) reported the presence of "*Er-*

likosaurus[sic] sp." from Iren Dabasu in Inner Mongolia, and they considered the Iren Dabasu fauna coeval with that of the Baynshin Tsav site. A frontal from the Judith River Formation of Canada first figured and described by Sues (1978), who did not assign it to any particular taxon in the absence of diagnostic features, was identified by Currie (1987a) as "cf. *Erlikosaurus*[sic]." However, Barsbold and Maryanska (1990) pointed out that the frontal bone of *Erlicosaurus andrewsi* is not diagnostic. Jerzykiewicz and Russell (1991) correlated the Baynshirenskaya Svita faunal assemblage with the Turonian to Campanian (Late Cretaceous) marine invertebrate stages, but there is little stratigraphic constraint on this correlation.

DIAGNOSIS: Because the skull described here is the only one known for any therizinosauroid, it is unclear at what taxonomic level its apomorphic features are diagnostic. Furthermore, without a precise hypothesis of relationship it is not possible to determine which characters shared with other Maniraptora are homologies and which are homoplasies diagnostic of *Erlicosaurus andrewsi* or a more inclusive clade of therizinosauroids.

In comparison with other nonavian coelurosaurian and maniraptoran theropods, the skull of *Erlicosaurus andrewsi* is distinguished by: edentulous premaxilla with sharp, vertical ventrolateral edge, extremely elongate nares due to regression of the maxilla, antorbital fossa with well-developed overhanging lip, medial wall of antorbital fossa extensive and imperforate, maxilla with medially inset dentition and few nutrient foramina on posterior part of facial process, posterior process of jugal covering anterior surface of quadratojugal, vomer extremely elongate and extending posteriorly to meet cultriform process, parabasisphenoid with extremely large pneumatic spaces, external auditory meatus restricted ventrally by lateral expansion of braincase, passage for internal carotid artery enclosed on occiput, trigeminal opening divides into three branches within side wall of braincase, and a homodont maxillary dentition of numerous (23) small, lanceolate, coarsely serrated, unrecurved, mediolaterally flattened teeth constricted at the base.

The dentary of *Erlicosaurus andrewsi* shares

Fig. 1.　Stereophotographs of the holotype skull of *Erlicosaurus andrewsi* in left lateral view. Abbreviations: aof antorbital fossa; f frontal; fit infratemporal fenestra; j jugal; l lacrimal; m maxilla; n nasal (right); pa palatine; pf prefrontal; pm premaxilla; po postorbital; pop paroccipital process; pt pterygoid; q quadrate; qj quadratojugal; spf subsidiary palatal fenestra; sq squamosal.

with that of the therizinosauroids *Alxasaurus elesitaiensis* and *Segnosaurus galbinensis* the unique features of a horizontal shelf lateral to the posterior tooth row and a heterodont dentition gradually changing from long, tapering, teeth without a basal constriction anteriorly to shorter, lanceolate, mediolaterally flattened teeth constricted at the base posteriorly.

In comparison with the two other therizinosauroids in which the dentary is known, that of *Erlicosaurus andrewsi* differs in having 31 teeth as opposed to approximately 40 in *Alxasaurus elesitaiensis* and 25 in *Segno-*
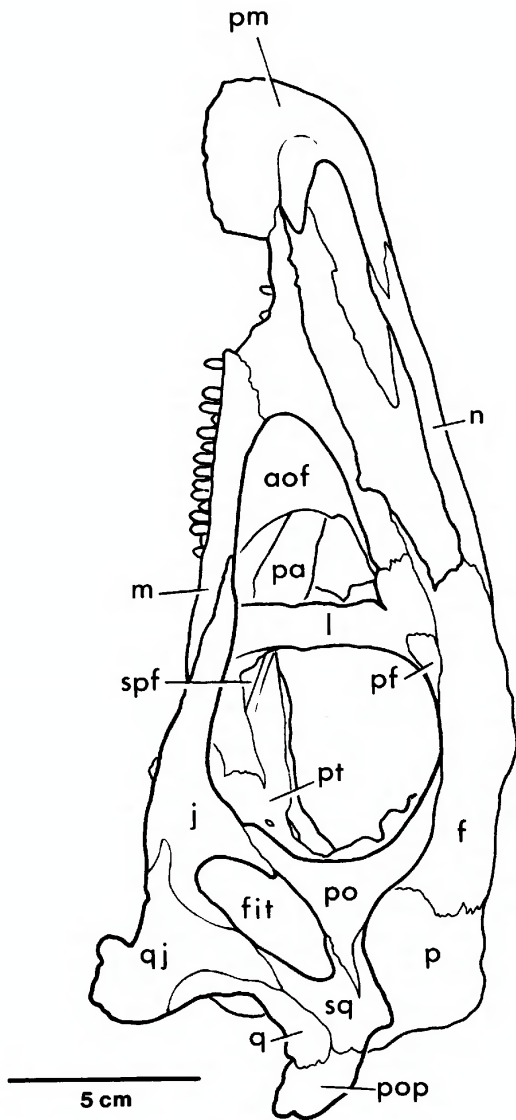
Fig. 1.　Continued.

of the tooth are coarser than those on the anterior, unlike those in *Erlicosaurus andrewsi* and *Alxasaurus elesitaiensis* where the serrations are similar on both edges. In *Alxasaurus elesitaiensis* and *Segnosaurus galbinensis* the teeth are slightly recurved, unlike in *Erlicosaurus andrewsi*. Finally, in *Segnosaurus galbinensis* the change from longer to shorter teeth takes place further posteriorly in the tooth row than in *Erlicosaurus andrewsi* (the condition in *Alxasaurus elesitaiensis* is unclear).

DESCRIPTION

In spite of its delicate construction, the skull is remarkably uncrushed (figs. 1–8). The premaxillary region is nearly undistorted, but the maxillary part of the rostrum is compressed slightly mediolaterally. This is most evident in the medial displacement of the right lacrimal and of both palatines, as discussed below. The skull is also twisted very slightly, as shown by the ventrolateral dislocation of the left frontal. The two hemimandibles are apparently uncrushed.

Every element is represented except the left nasal and both stapes, although the only ectopterygoid preserved is incomplete. The right side of the braincase and skull roof and part of the left exoccipital region were separated from the rest of the skull. The distal part of the right quadrate and the right lateral part of the basisphenoid were cut away from this piece and are also preserved separately. The two hemimandibles are preserved separately, and the posterior part of the right hemimandible is missing.

ROSTRUM

The right **premaxilla** is nearly complete, but the left element is incomplete posteriorly and posterodorsally and is damaged on its anterior surface (figs. 1–4). The main portion of the premaxilla is approximately half as broad as it is long. The narial process is subvertical at its base and bends posteriorly to become subhorizontal above the nares. The palatal surface of the premaxilla is strongly concave, and the labial margin forms a sharp, thin edge.

The vascularized surface of the premaxilla, its lack of teeth, and its sharp ventrolateral

saurus galbinensis. Furthermore, the dentaries of *Erlicosaurus andrewsi* and *Segnosaurus galbinensis* lack teeth in the symphyseal region while that of *Alxasaurus elesitaiensis* possesses them, and a horizontal shelf on the dorsal edge of the dentary lateral to the tooth row arises further anteriorly in *Erlicosaurus andrewsi* (opposite the fifth tooth) than in the other two genera. The serrations on the teeth of *Alxasaurus elesitaiensis* are coarser than those of *Erlicosaurus andrewsi* and *Segnosaurus galbinensis,* and in *Segnosaurus galbinensis* the serrations on the posterior edge
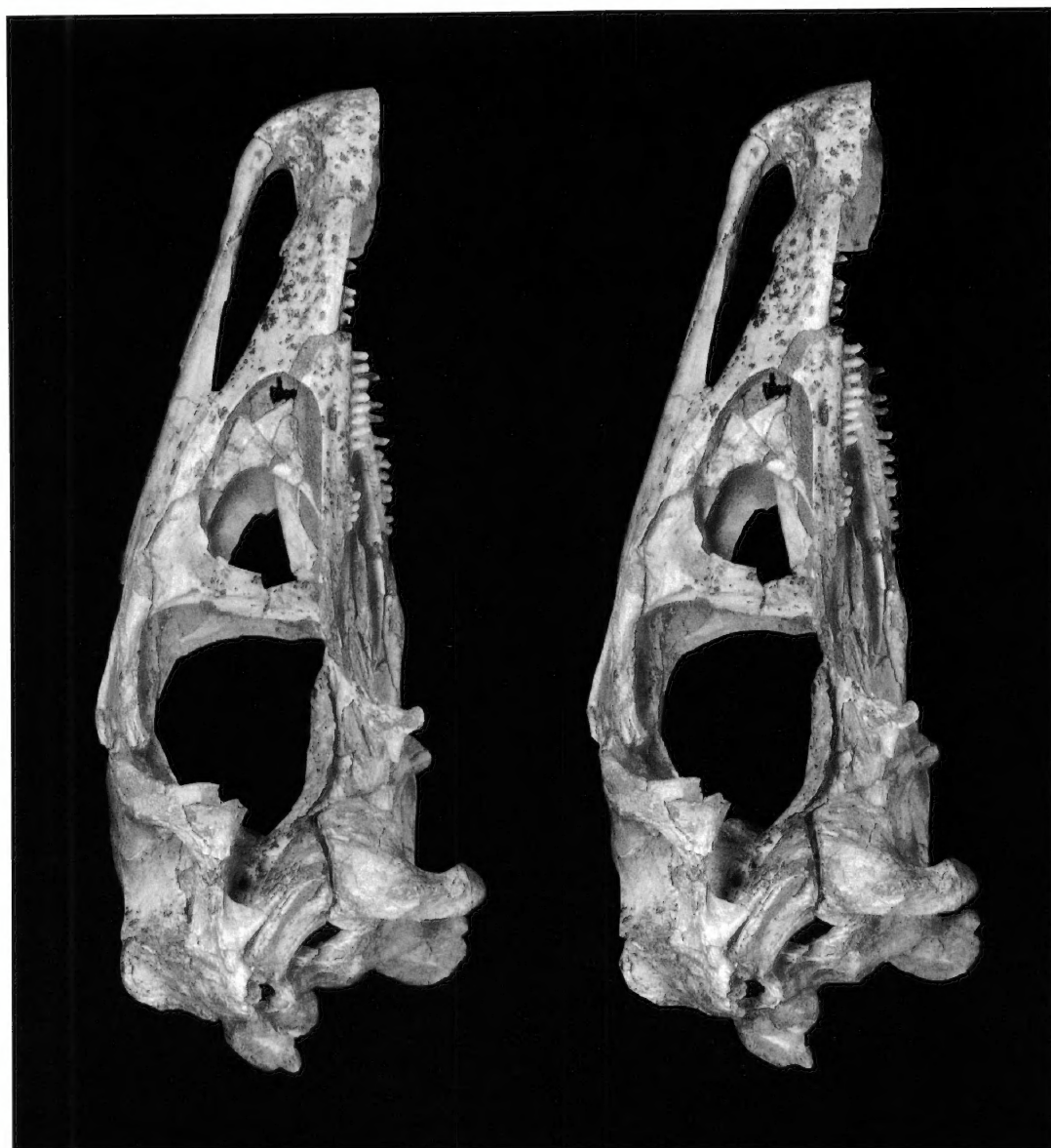
Fig. 2. Stereophotographs of the holotype skull of *Erlicosaurus andrewsi* in right lateral view. Abbreviations: aof antorbital fossa; l lacrimal; m maxilla; n nasal; pf prefrontal; pm premaxilla; po postorbital; q quadrate; scl scleral ossicles; sq squamosal; tf transverse flange of pterygoid.

margin indicate that a keratinous structure probably covered the end of the rostrum. The nearly vertical ventrolateral margin of the premaxilla is continuous with a ridge on the anterior end of the ventrolateral margin of the maxilla, and together they form a sharp edge that descends anteriorly to lie at the same level as the ventral edge of the maxillary tooth row. Near the anterior midline the edge of the premaxilla regresses slightly dorsally, and it bears distinct bony "denticles" immediately lateral to this notch. The shape of the labial margin of the premaxilla suggests that the keratinous structure had an even, regular edge lacking a sharp beak at its tip.

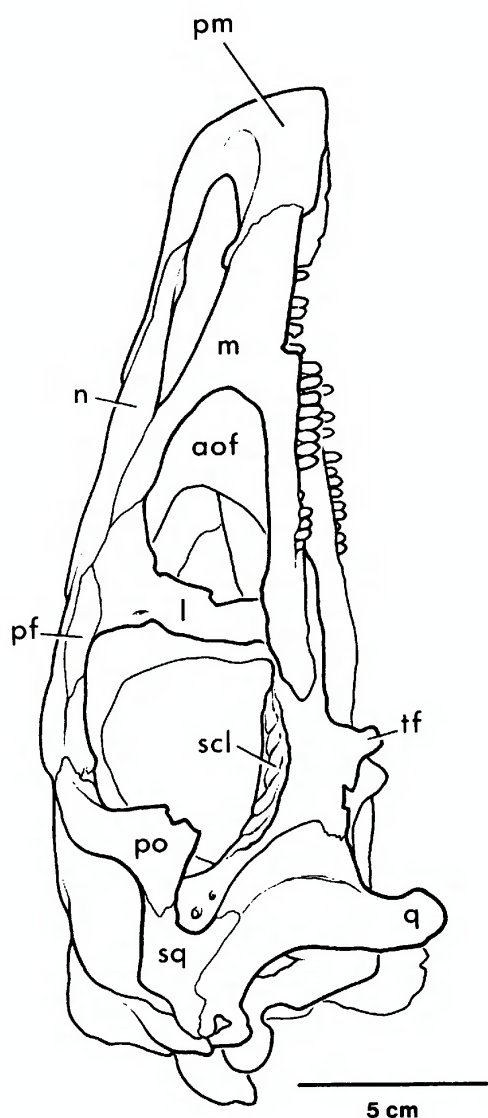Sixteen vascular foramina are situated on

Fig. 2. Continued.

Within the nares, three large foramina open from the dorsal surface of the right premaxilla. The dorsalmost of these opens dorsally onto the base of the narial process. Another foramen posteroventral to the first opens posteriorly from the dorsal surface, as does a smaller foramen posterolateral to the latter.

Four large (~2 mm diameter) foramina pierce the palatal surface of the right premaxilla anteriorly near the midline. Three of these border on the incisive foramen, the fourth is lateral to the middle of these three. A fifth small foramen lies anteroventral to the latter.

The left premaxilla is broken anteriorly, revealing canals within the bone connecting many of the foramina on the face and palate and within the narial chamber. It is impossible to determine the precise extent of these connections, but all may be interconnected via a large, matrix-filled cavity within the body of the premaxilla.

The premaxillae form a slitlike incisive foramen immediately posterior to the anterior end of the rostrum (fig. 4). The flat, obliquely oriented medial surface of the premaxilla within the slit converges dorsally with its opposite, meeting at the base of the narial process. A passage leads from the incisive foramen posterodorsally into the narial chamber, where it enters a shallow groove on the dorsal surface of the posterior part of the premaxilla. Posterior to the incisive foramen the premaxillae form an extensive, flat secondary palate extending posteriorly to meet the vomer opposite the anteriormost maxillary tooth, although this region is poorly preserved. The premaxillae, thus, meet at the midline of the palate over the posterior half of their length. The contact between the premaxilla and maxilla on the palate is poorly preserved, but it generally extends anterolaterally away from the midline. The premaxilla underlies the maxilla along this contact.

The presence of a subnarial foramen between the premaxilla and maxilla cannot be determined. The expected position of this foramen, near the lateralmost part of the narial depression, is preserved only on the right side. There is a matrix-filled gap between the two bones in this region (fig. 3), positioned mainly within the premaxilla, but the edges of the surrounding bone appear to be broken.

the external surface of the right premaxilla. They are dominated by a series of eight large (~1 mm in diameter) foramina aligned along a dorsally concave arc extending from the base of the narial process posteriorly to within the narial region. A large anterodorsal foramen opens dorsally, whereas the five foramina that form the anterior part of the arc open ventrally, and the posteriormost two foramina open posteriorly. The other foramina, dorsal to those forming an arc, open directly outward.

Fig. 3.   Stereophotographs of the holotype skull of *Erlicosaurus andrewsi* in dorsal view. Abbreviations: bc coossified braincase; f frontal; fs? possible subnarial foramen; m maxilla; n nasal; p parietal; pf prefrontal; pm premaxilla; po postorbital; sq squamosal.

The narial process of the premaxilla is very long, extending posterodorsally to terminate opposite the anterior margin of the antorbital fenestra. The posterior end of the most complete element, the right, is broken, and the depressed dorsal surface of the nasal with which it articulates indicates that the premaxilla extended approximately 1 cm further, to a level opposite the posterior end of the nares. The premaxillae alone form the anterior half of the internarial bar, and posteriorly the narial process overlies the nasal on the posterior half. The internarial bar is nearly circular in cross section at its base and flattens posterodorsally. Immediately anterior to the nasal, the dorsal surface of the
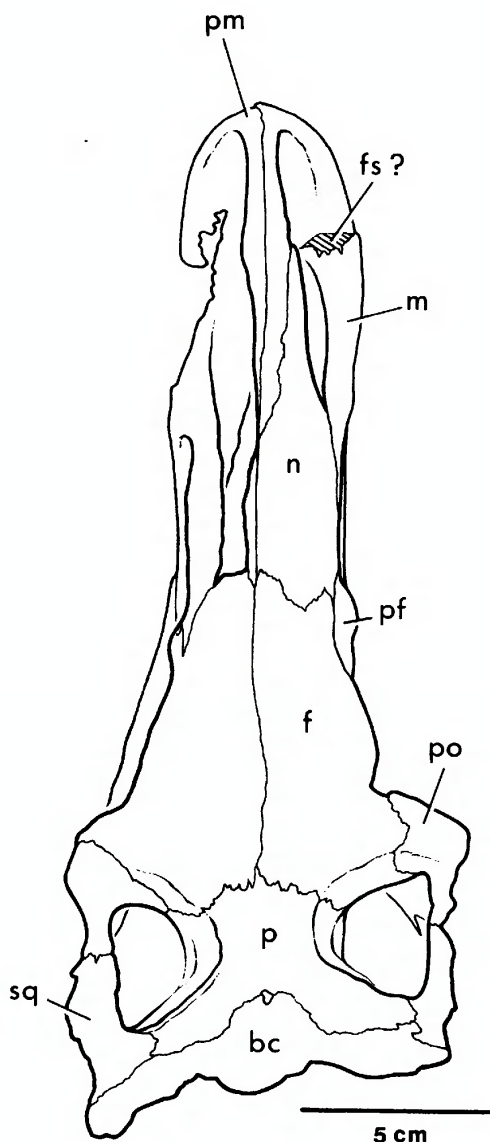
Fig. 3.   Continued.

overlaps the dorsal surface of the maxilla, and it ends bluntly at a level opposite the anteriormost maxillary tooth. The maxillary process, thus, does not contact the nasal posterodorsally.

The **maxillae** are both nearly complete, although the facial process of the left element is missing anterior to the tooth row (figs. 1–5). The right element is broken beneath the anterior end of the antorbital fenestra, and posterior to the break it is dislocated ventrally and medially a few millimeters.

The external surface of the facial process anterior to the antorbital fenestra is pierced by at least 11 external maxillary foramina. Many of these are oval, with the long axis extending posterodorsally. The largest foramen (~2 mm diameter) is above the 13th tooth position, immediately ventral to the antorbital fenestra, and it exits anteriorly (fig. 5). A much smaller foramen lies dorsal to the penultimate teeth of the right maxilla but is lacking from the left maxilla.

A ridge continuous anteriorly with the ventral margin of the premaxilla arises posteriorly from the lateral surface of the facial process dorsal to the sixth tooth position. It enlarges anteriorly and gradually becomes ventrolaterally directed, coming to lie lateral to the anterior end of the tooth row.

The ventral surface of the maxilla is nearly flat posterior to the tooth row, facing ventrally and slightly laterally (fig. 4). Anteriorly it gradually becomes vertical, so that medial to the posterior part of the tooth row it faces ventromedially and lateral to these teeth it faces ventrolaterally. The ventrolateral surface becomes vertical anteriorly, whereas the ventromedial surface becomes horizontal with a gentle ventromedial concavity, and it broadens to form a palatal shelf meeting the vomer and premaxilla anteriorly.

The maxilla forms the anterior and ventral borders of the antorbital fossa, part of the dorsal border, and a thin wall medial to the anterior half of the fossa (fig. 5). This medial wall appears to lack the accessory antorbital fenestra typical of nearly all nonavian theropods, but matrix covers some areas of the bone and it is possible that a fenestra is actually present. A matrix-filled opening on the left side (fig. 1) is suggestive of this fenestra, but its edges are broken, and a fenestra is

narial process is gently fluted over a 2-cm-long region.

The maxillary process of the premaxilla overlies the anterior end of the maxilla. This process floors the anterior end of the narial cavity, where it is dorsolaterally concave. Medially, the process curves dorsally to become nearly vertical. The medial edge of each side does not meet its opposite at the midline, and the two sides diverge posteriorly from the internarial bar, tapering in height as well. Posteriorly, the maxillary process broadly
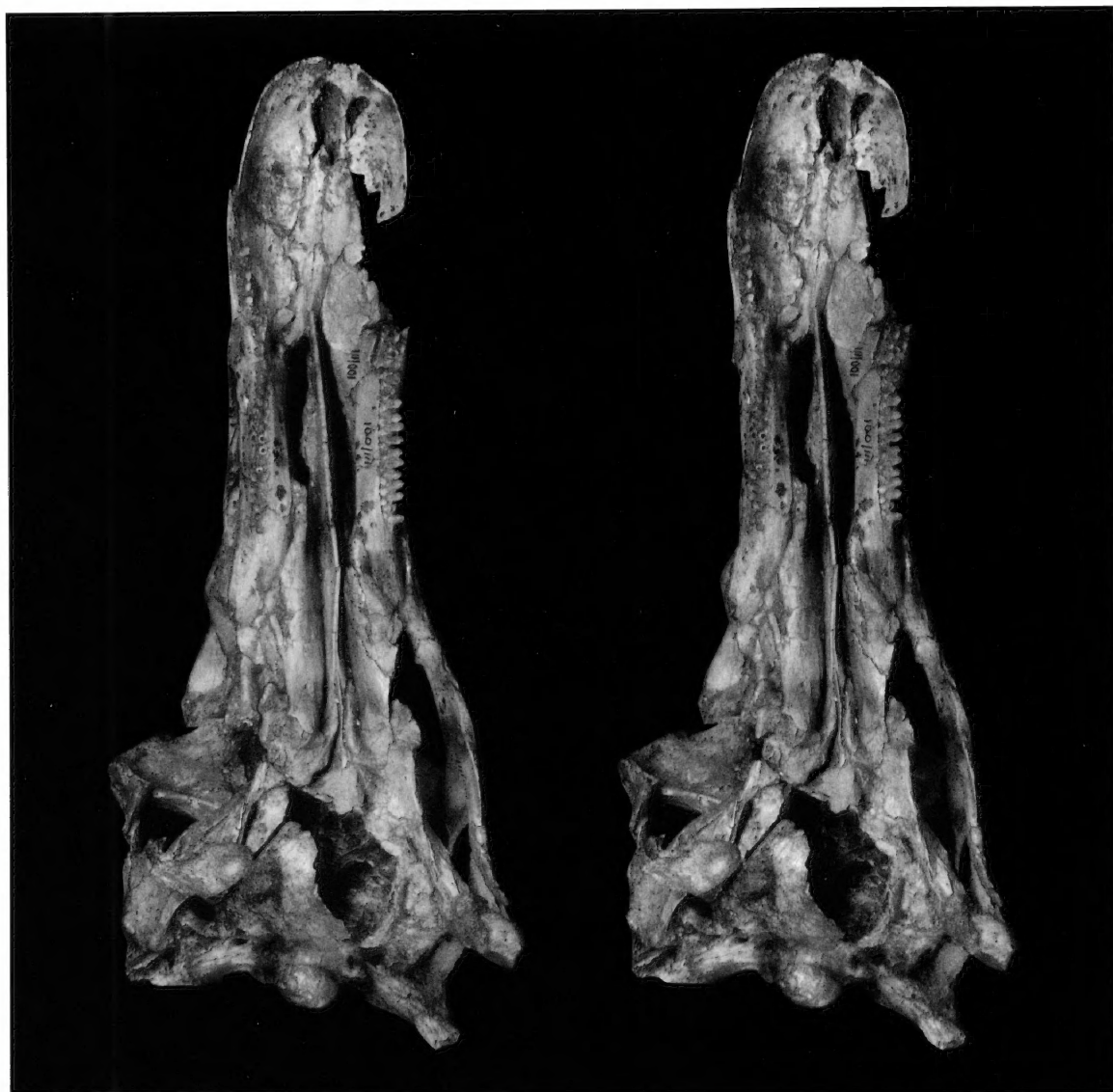
Fig. 4. Stereophotographs of the holotype skull of *Erlicosaurus andrewsi* in ventral view. Abbreviations: bc coossified braincase; c choana; eam external auditory meatus; ec ectopterygoid; fi incisive foramen; j jugal; m maxilla; pa palatine; pm premaxilla; pt pterygoid; q quadrate; v vomer.

absent in the same position on the right side (fig. 2). If a fenestra is hidden beneath matrix, it is unusually small and unusually anterior or ventral in position.

The posterior edge of this wall is gently concave posteriorly. A lateral lip overhangs the dorsal, anterior, and ventral borders of the fossa, and the dorsal lip is continuous with a similar lip on the lacrimal posteriorly. The floor of the fossa is marked by a longi-

tudinal row of three small ($\sim$5 mm diameter) but deep pockets.

The medial surface of the maxilla borders the extremely large, elongate choanal opening (fig. 4). Posteriorly, opposite the posterior end of the tooth row, its medial surface contacts the palatine, which underlies its flattened posterior part. The maxilla is overlain laterally by the jugal, which also sends a short process over the dorsal surface of the poste-
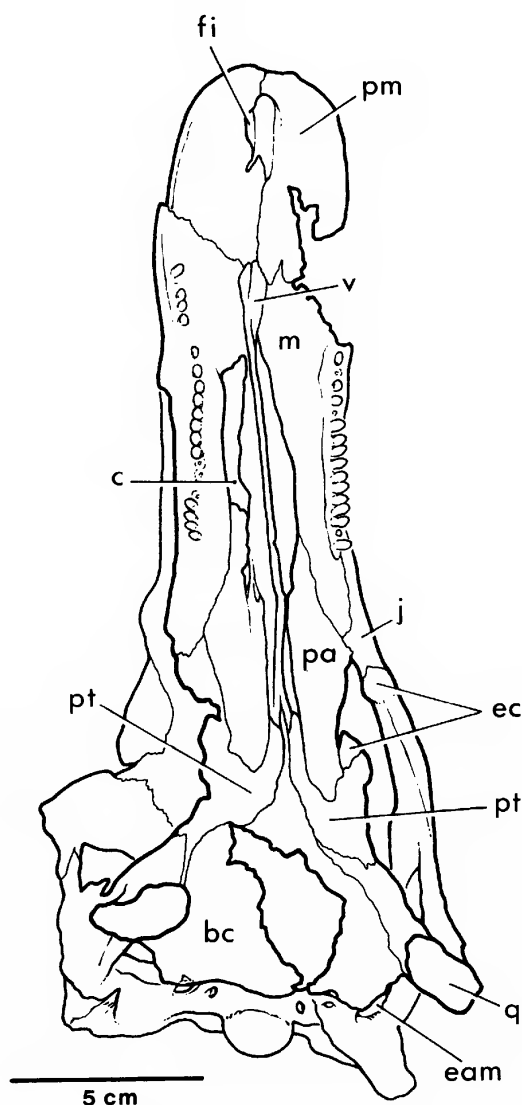
Fig. 4.   Continued.

end, and forms the ventrolateral border of the posterior half of the nares. The facial process of the maxilla is dorsolaterally oriented anterior to the antorbital fenestra, and posterodorsally it gradually becomes nearly vertical.

The **nasal** is long, extending from the level of the anterior end of the orbit to slightly past the middle of the internarial bar (figs. 1–3). It is dorsally convex in cross section, and both elements together form a gentle depression along the dorsal midline. The nasal is nearly twice as broad posterior to the narial opening as it is medial to it, and it tapers anteriorly. The narial process of the premaxilla overlies it anteriorly, fitting into a longitudinal depression on the medial half of the nasal. The posterior end of the nasal is rounded in dorsal view and overlaps the anterior end of the frontal. It abuts the prefrontal over a small area posteriorly, and overlies the anterior two-thirds of the lacrimal. It abuts the maxilla ventrolaterally, and it sends a short anteroventral process along the dorsal edge of the maxilla at the posterior end of the narial opening, so that the nasal forms the entire posterior corner of the opening. Foramina are present on the posterolateral part of its dorsal surface only, opening either anteriorly or posteriorly.

The **lacrimal** forms the entire preorbital bar separating the orbit from the antorbital fenestra (figs. 1, 2, 5). The ventral part of each element has been dislocated medially and is no longer in articulation with the maxilla and jugal. The dorsal part of the right lacrimal is displaced medially, and the dorsal borders of the left are difficult to interpret due to the absence of the left nasal and damage to this part of the lacrimal. It is therefore not possible to be certain whether the entire dorsal surface of the lacrimal is covered by the prefrontal and nasal, as would appear from a dorsal view of the skull (fig. 3). The dorsal part of the bone bends medially to form a broad shelf, best seen on the right element, and this would be exposed dorsally if the bone had not been dislocated medially. It is difficult to determine the extent of this dorsal exposure, however. A posterior process of the dorsal part of the lacrimal, as in Dromaeosauridae, is lacking.

The large (~5 mm high, 3 mm wide) lac-

rior part of the maxilla. This medial process of the jugal appears to contact the palatine, thus excluding the maxilla from the small suborbital fenestra (fig. 6). It is unclear whether the ventral edge of the lacrimal contacts the maxilla; if so, it is only over a brief area anterior to the end of the jugal.

The facial process of the maxilla extends posterodorsally to end abruptly dorsal to the anterior edge of the antorbital fenestra. Here it overlies the lacrimal laterally. It abuts the nasal medially, contacting the latter from the posterior end of the nares to its own poste-

Fig. 5.   Left antorbital region of the holotype skull of *Erlicosaurus andrewsi* in lateral view. Abbreviations: fme external maxillary fenestra; j jugal; l lacrimal; m maxilla; pa palatine; pf prefrontal; pt pterygoid; spf subsidiary palatal fenestra.

rimal foramen lies posteriorly near the top of the preorbital bar from within a depression. Ventral to the foramen the lacrimal broadens mediolaterally to form a flat surface facing slightly posterolateral. This surface narrows ventrally, and the ventral contact with the jugal and, perhaps, maxilla is essentially longitudinal. Within the antorbital fossa the anterodorsal part of the lacrimal is excavated along its ventral surface, continuous with the excavation on the dorsal part of the maxilla. The dorsal half of the preorbital bar is also excavated on its anterior surface. A lateral lip is thus formed around the antorbital fossa along every edge except the posteroventral.

The **prefrontal** is a small, robust bone at the anterodorsal corner of the orbit (figs. 1–3). In dorsal view it is triangular, with a lateral apex and a broad medial base. Its posterolateral edge is longer than its anterolateral edge, but the precise extent of the anterior part is unclear due to damage. It underlies the frontal along its entire medial surface and briefly contacts the nasal anteriorly. Anteriorly it overlies the lacrimal, and it also abuts the lacrimal along its anterolateral edge. Its dorsal surface is smooth, but its posterolateral edge is rugose, continuous with the rugose orbital rim of the frontal.

ORBITAL AND TEMPORAL REGIONS

The left **jugal** is articulated with the skull (fig. 1), and the right element is preserved separately along with the quadratojugal. The suborbital process is long and slender, arching dorsally so that it has a gently concave ventral edge. It extends to the anterior end of the orbit, where an articulation surface on the left jugal demonstrates that it underlies the lacrimal, which has been dislocated on the specimen. It overlaps the maxilla laterally, and a medial process extending from the articulation with the lacrimal overlaps the dorsal surface of the maxilla. This process tapers medially and approaches the palatine without, apparently, meeting it. From beneath the postorbital bar to midway beneath the orbit the ventral edge of the jugal is roughened and somewhat broadened for the origin of M. adductor mandibulae externus.

A small bone adhering to the medial surface of the left jugal is apparently the lateral part of the ectopterygoid (fig. 6). Its contact is posterior to the maxilla, so that the jugal would have formed the medial edge of a small suborbital fenestra.

The ascending process of the jugal forms the ventral half of the postorbital bar. It ex-
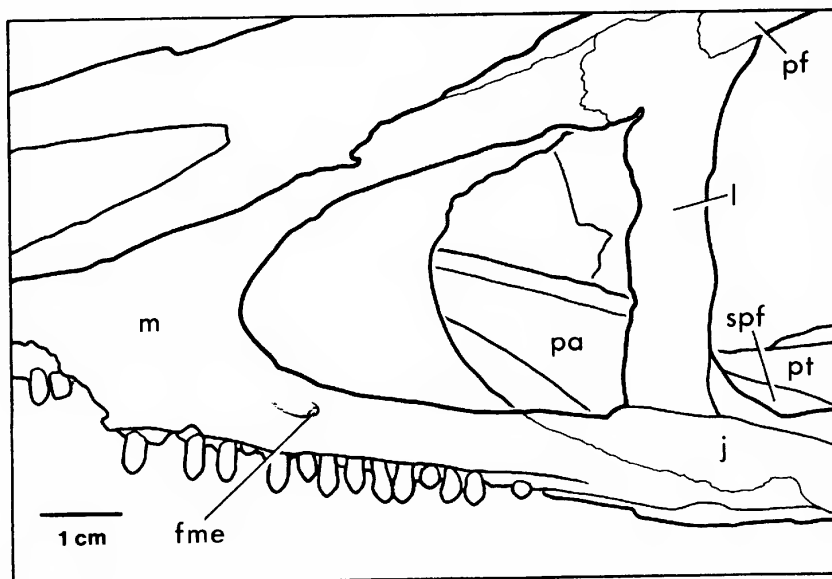
Fig. 5. Continued.

tends posterodorsally to underlie the posteroventral edge of the postorbital. The jugal broadens at this contact, and a ridge extending longitudinally along the contact surface fits into a depression in the corresponding surface on the postorbital. The lateral surface of the ascending process is flat and continuous with the body of the jugal, but on the medial surface the posterior base of the process is medially concave. The body of the jugal is also medially concave between the base of the ascending process and the muscle scar on its ventral edge. The ascending process parallels, rather than approaches, the ascending process of the quadratojugal so that the infratemporal fenestra is not constricted.

The posterior end of the jugal has a complex contact with the quadratojugal. A narrow anterior process of the quadratojugal fits into a groove on the lateral surface of the jugal extending forward to beneath the postorbital bar. The quadratojugal also sends a short, broad anterior process along the medial surface of the jugal. The jugal briefly ascends dorsally along the quadratojugal, forming the posteroventral corner of the infratemporal fenestra, where it overlies the quadratojugal laterally.

The **frontal** extends from above the pos-

terior end of the antorbital fenestra posteriorly to the anteromedial corner of the supratemporal fossa (figs. 1–3). It is dorsally convex near the midline, becomes dorsally concave laterally, and has an upturned lateral margin above the orbit. In lateral view it is gently convex dorsally. Anteriorly it underlies the nasal and overlies the prefrontal, possibly with a brief contact with the lacrimal. Above the orbit its lateral border is rugose and dorsally convex. Its dorsal surface descends posteriorly to face posterolaterally within the supratemporal fossa. The postorbital overlies this posterolateral face, and the suture is extensive. The lateral edge of the frontal is extremely rugose immediately anterior to the postorbital. Posteriorly, the frontal is strongly sutured to the parietal, and the contact is posteriorly concave in dorsal view. Both the frontal and the parietal are raised over a brief (~5 mm long) area along their mutual contact near the top of the supratemporal fossa. The parietal also sends an anterior process beneath the posterior part of the frontal on the anterior wall of the supratemporal fossa, so that the posteriormost part of the frontal rests partly upon the parietal in addition to its main contact with the capitate process of the laterosphenoid. In dorsal view, the lateral

Fig. 6.   Posterior part of the palate of the holotype skull of *Erlicosaurus andrewsi* in ventral view. Abbreviations: bs basisphenoid portion of coossified braincase; cp cultriform process; ec ectopterygoid; j jugal; m maxilla; pa palatine; pt pterygoid; tf transverse flange of pterygoid; v vomer.

edge of the frontal is straight except for a lateral excursion at the posterior end of the orbit.

Unlike that in most dinosaurs, the posterior edge of the frontal lacks a depression within the supratemporal fenestra for the origin of the mandibular adductor musculature. Instead, the posterior edge of the frontal within the fenestra is nearly vertical, facing posterolaterally and slightly dorsally.

A broad descending process of the frontal forms the posterodorsal wall of the orbit. It faces anteroventrally and extends laterally to meet the capitate process of the laterosphenoid. The cristae cranii are poorly developed on the ventral surface of the frontals. Each has a gently rounded ventral margin, and the cristae are broadly separated, as in *Troodon formosus* Leidy, 1856 (see Hopson, 1979), indicating moderately large olfactory lobes of the brain.

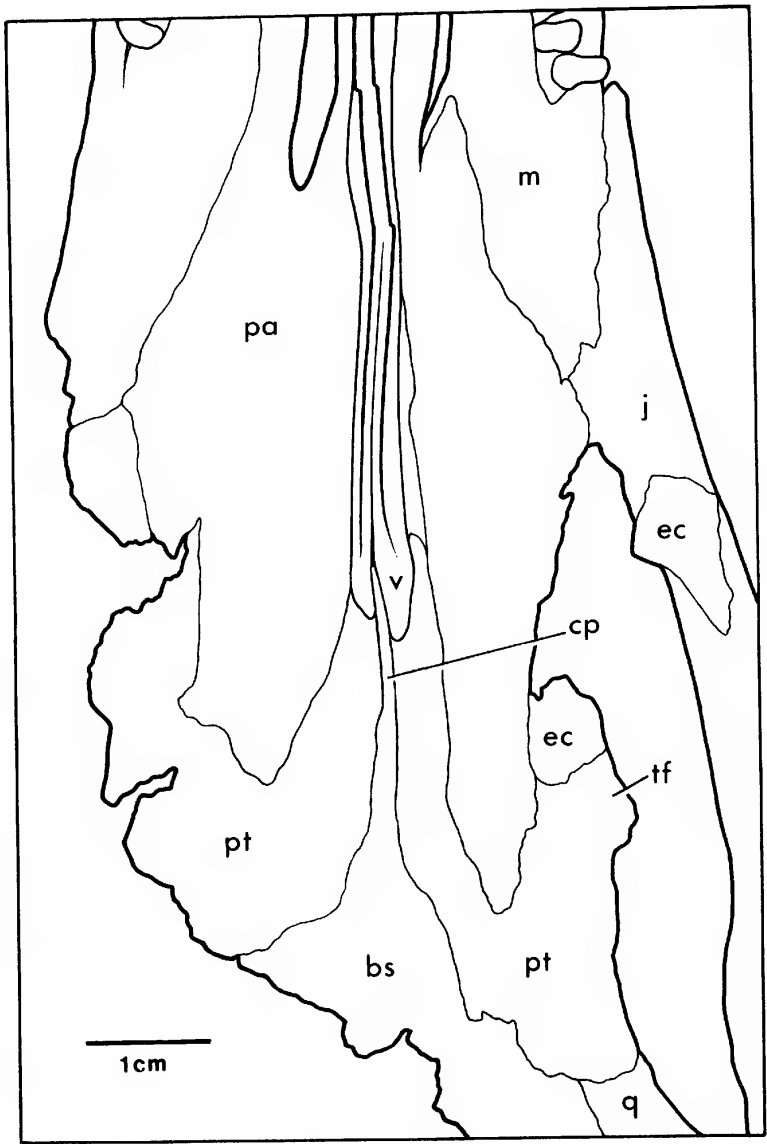The fossa for the cerebrum on the ventral

Fig. 6. Continued.

surface of the postorbital process of the frontal is relatively larger than in most nonavialian dinosaurs. Although it was not possible to make an accurate endocast of the braincase, direct comparison with specimens of other taxa reveals that it is much larger than in *Plateosaurus engelhardti* Meyer, 1837 (AMNH 6810) and similar in size to those for *Velociraptor mongoliensis* Osborn, 1924 (MAE 298) and *Troodon formosus* (AMNH 6174).

The **parietals** appear to be fused, although a series of tiny cracks near the midline may represent a suture. The parietal is short and stout, with a flat dorsal surface lacking a sagittal crest (figs. 1–3, 7). Its dorsal surface is horizontal, continuous with that of the frontal, rather than flexing at the contact and facing posterodorsally, as in many Maniraptora.

A well-developed lambdoidal crest forms a sharp dorsal edge to the posterolateral process of the parietal. Where this process meets
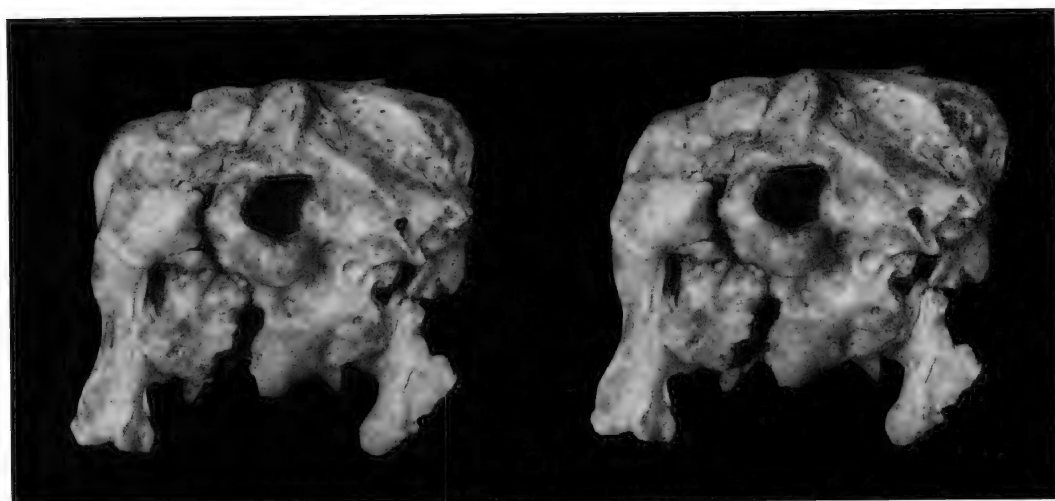
Fig. 7.   Occiput of the holotype skull of *Erlicosaurus andrewsi* in posterior view. Abbreviations: eam external auditory meatus; fc foramen for internal carotid artery; fe? possible location of foramen for eustachian tube; fm foramen magnum; fv foramen vagi; p parietal; q quadrate; qj quadratojugal; XII lateral hypoglossal foramen.

the body of the parietal the crest forks, forming a brief crest extending along the dorsomedial rim of the supratemporal fossa and a crest extending medially a short distance. The anterolateral surface of the posterolateral process is nearly vertical, forming the posterior wall of the supratemporal fossa. The posteromedial surface of this process forms much of the dorsal part of the occiput, and faces slightly dorsally.

The occipital portion of the parietal contacts the dorsolateral edge of the supraoccipital and the dorsal edge of the paroccipital process, so that a posttemporal fenestra is either absent or reduced to a small opening (fig. 7). A small opening dorsolateral to the supraoccipital on the right side seems to be a result of damage, but a small opening beneath the occipital portion of the squamosal appears to be real. In posterodorsal view, the parietal expands in breadth laterally on the occiput and then tapers distal to the supraoccipital. The posterolateral process articulates with the squamosal distally, but both bones are damaged at their contact. Within the supratemporal fossa, the parietal rests upon the laterosphenoid anteriorly and the prootic posteriorly. The parietal sends a slender process anteriorly between the laterosphenoid and the frontal to contact the postorbital. The

posterior edge of the parietal is notched along the midline in dorsal view, bordering a small (~5 mm diameter) opening between it and the supraoccipital.

Both **squamosals** are damaged medially but are otherwise complete (figs. 1–3). An anterior process has a sharp dorsal edge that is continuous with the lambdoidal crest of the parietal. It forms the posterolateral border of the supratemporal fossa and is nearly vertical, facing slightly dorsolaterally. It contacts the postorbital anteriorly, and a slender posterior process of the postorbital lies in a groove on the dorsolateral surface of the squamosal. A longitudinal crest is formed on the ventral part of the lateral surface beneath the posterior process from the postorbital, and extends posteriorly nearly the length of the squamosal. The posteriormost part of the lateral surface of the squamosal is rugose, with longitudinally aligned small ridges.

The descending process of the squamosal extends midway down the posterior border of the infratemporal fenestra. A ridge is formed along the anterior edge of the descending process laterally, and the squamosal broadly overlaps the anterior surface of the quadrate medially. In lateral view, the contact between the squamosal and quadrate is nearly flat, but the medial part of the de-
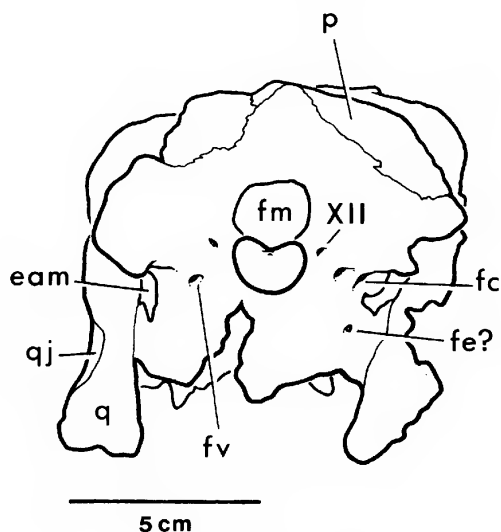
5 cm

Fig. 7.   Continued.

scending process is gently convex anteriorly. Ventrally, the descending process is overlapped laterally by the ascending process of the quadratojugal.

The medial process of the squamosal is poorly preserved, and its broad occipital surface is fragmented. It overlaps the parietal anteriorly and overlies the distal end of the paroccipital process. A small opening is present between the right element and the anterodorsal edge of the paroccipital process, but a similar opening is absent on the left side. The articulation with the quadrate is not exposed, both quadrates being in articulation, but it appears to be mediolaterally broader anteriorly than posteriorly. The articulation is well lateral of the side wall of the braincase, as is primitive in theropods, unlike the more medial articulation of birds and, to a lesser extent, troodontids. The squamosal sends a brief process ventrally along the anterior edge of the paroccipital process, but the quadrate may articulate in part with the latter.

The **postorbital** is triradiate, with processes extending ventrally, posteriorly, and medially (figs. 1–3). The descending process forms the dorsal half of the postorbital bar, overlying the ascending process of the jugal anterodorsally, as described above. The descending process has a broad, nearly flat

anterior surface and tapers posteriorly. Dorsally, the anterior surface of the descending process curves anteriorly and broadens medially to become continuous with the medial process. The body of the postorbital, at the confluence of the three processes, is posteriorly convex and broadly covers the posterior surface of the orbital process of the frontal. Dorsal to the base of the posterior process the surface of the postorbital is rugose, with transversely oriented ridges. The medial process is narrower than the body, and forms the ventral half of the anterior wall of the supratemporal fossa beneath the frontal. The posterior process tapers sharply in height posteriorly and sends a narrow process posteriorly onto the lateral surface of the squamosal.

The **quadrate** comprises an extensive orbital process, a tall body, a short dorsal process, and a large mandibular process (figs. 1, 2, 4, 7). The orbital process covers the ventral part of the lateral surface of the braincase. It overlies the pterygoid, the greatly expanded basisphenoid, and the ventral part of the prootic. The braincase bulges outward here, and the orbital process is anterolaterally convex. Its dorsal edge descends anteriorly to beneath the trigeminal foramen, where it levels off and then terminates. The anterior edge of the orbital process is nearly straight. The ventral edge curves complexly as it wraps across the ventrolateral edge of the braincase.

The body of the quadrate is broad dorsal to the large quadrate foramen. This portion faces posteriorly and somewhat laterally. Its posterolateral surface is smooth and slightly concave. It is subrectangular in shape, taller than broad, with a slightly convex lateral edge.

The quadrate forms the medial border of a large quadrate foramen (fig. 7). The foramen is about three times as tall as it is wide. The quadrate is constricted to about half the width of its dorsal part medial to the foramen.

The mandibular process is oriented obliquely at about a 45° angle relative to the sagittal plane, the medial part being further anterior than the lateral part (fig. 4). The process ends about 2 cm below the level of the braincase and tooth row. A ridge descends from the posteromedial edge of the quadrate to the posterolateral edge of the mandibular process.

The mandibular articulating surface of the quadrate has three condyles—a large lateral condyle and two smaller medial condyles. The oval lateral condyle comprises about half the width of the surface, with which its long axis is aligned. The medialmost condyle is about two-thirds the width of the lateral condyle and is aligned transversely, oblique to the general orientation of the mandibular process. The third condyle lies between the two others on the posterior edge of the articulation surface. It is about half the size of the medial condyle and is aligned perpendicular to the long axis of the mandibular process. All of the condyles are well developed and strongly convex ventrally.

There is no evidence for a siphonial opening on the quadrate, although the areas in which one might occur are only preserved on the left quadrate, and these bone surfaces are fragmented. If a foramen is present it would either lie near the distal end of the bone, opposite the siphonial opening on the articular as in Crocodylia, or in the middle of the bone, as in birds. If it is distal it would exit from the posteromedial surface of the quadrate near the distal margin. A brief vertical ridge is formed in the middle of this surface, and a small depression on its lateral edge is in a position that might correspond to the siphonial opening. There does not appear to be a foramen within the depression, but the area is too poorly preserved to be certain. If the foramen is in the middle of the bone it would lie medial to the quadrate foramen. This area has been slightly crushed transversely, and although a foramen is not evident a small foramen could have been obliterated by crushing. In any case, if a foramen is present it is small.

The **quadratojugal** overlies the lateral edge of the quadrate, forming the lateral border of the quadrate foramen (fig. 1). It is triradiate, with a broad posterior process and slender anterior and dorsal processes, and has a nearly straight ventral edge. The posterior process covers most of the lateral surface of the mandibular process of the quadrate and ends bluntly. The slender anterior process extends between posterior tongues of the jugal on its lateral surface, and a broader process extends anteriorly medial to the jugal. The dorsal process, which is oriented slightly posteriorly, is

very broad ventrally. It narrows abruptly at the dorsal edge of the quadrate foramen and continues only a short distance further dorsally to meet the squamosal. The anterior edge of the dorsal process is nearly straight, but the posterior edge is strongly concave where it borders the quadrate foramen.

Scleral ossicles are preserved in the right orbit, overlying the pterygoid (fig. 2). Seven complete and one fragmentary ossicle are preserved in articulation. Each ossicle is subrectangular in shape, with parallel outer edges and convex anterior and posterior edges that overlap adjoining ossicles. The exposed, inner surface of each ossicle is slightly convex longitudinally.

PALATE

Both **palatines** are completely preserved (figs. 4, 6), but this part of the skull has been compressed mediolaterally so that the medial part of each bone is now vertical rather than horizontal. The lateral part of each palatine underlies the maxilla and ends anteriorly opposite the posterior end of the tooth row. It extends posterolaterally along the posteromedial edge of the maxilla to the area where a suborbital fenestra would be expected (see below). There is some indication of a foramen opening anteriorly on the palatal surface of the lateralmost part of the left palatine. Posterior to its contact with the maxilla the palatine becomes more vertical. It contacts the medial surface of the pterygoid flange and the ventromedial surface of the ectopterygoid.

The posterior portion of the palatine curves dorsomedially to become vertical. The dorsolateral surface of this posterior part of the palatine is thus longitudinally concave. It overlies that part of the pterygoid medial to the lateral flange. In lateral view, the posterior part of the palatine is highest posteriorly and descends in height in the anterior part of the orbit.

Most of the anterior part of the palatine is nearly vertical, but dorsally it bends medially to meet the opposite element along the midline. The contact between the palatines is long, extending from opposite one end of the antorbital fossa to the other. This part of the palatine comprises an anteriorly directed blade,

with a very gently concave anteroventral edge, a straight dorsal edge, and a convex posterodorsal edge. All surfaces of the palatines are smooth, and there is no evidence of pneumatic sinuses within the bone.

Although a subsidiary fenestra between the palatine and pterygoid (Gauthier, 1986: 26) is not visible in ventral view, its presence is indicated by an indentation along the dorsally bent medial edge of the palatine, evident in dorsolateral view (figs. 1, 5). The fenestra appears to extend from opposite the anterior end of the orbit posteriorly about half the length of the orbit.

The **pterygoids** are both preserved, but the posteriormost part of the left element is damaged (figs. 4, 6). The quadrate ramus is hidden beneath the quadrate, but it appears to be short, high, and vertical. It is tightly compressed between the quadrate and the expanded basisphenoid. There is no evidence of a basipterygoid joint with the basisphenoid, although this area is damaged on the left side and incomplete on the right. Furthermore, the pterygoid articulates with the entire anterolateral edge of the braincase rather than only at the basipterygoid joint. This strongly suggests that this region of the skull was akinetic.

The pterygoid broadens and becomes ventromedially oriented anterior to the quadrate ramus. A short but stout transverse flange extends ventrolaterally from the anterior end of this broad area. The pterygoid forms the posterior half of an oval articulating surface on the lateral surface of the flange, the ectopterygoid forming the anterior half.

Medial to the flange the pterygoid narrows and forms an anteriorly directed blade. This blade rises anteriorly and tapers in height, ending at the anterior end of the orbit. It has a concave lateral surface. The pterygoids are separated by the cultriform process of the parabasisphenoid ventrally, but dorsally the two elements meet along the midline.

Only the left **ectopterygoid** is present, and it is incomplete anteriorly (figs. 4, 6). The posterior part of the bone is very robust and forms the anterior half of the transverse flange. A posteriorly curving piece of bone posterior to the posteriormost part of the maxilla on the medial surface of the jugal also probably belongs to the ectopterygoid. If so, the ecto-

pterygoid was greatly elongate medially, and it formed the posterior edge of a small suborbital fenestra.

The single **vomer** is extremely long, extending from between the transverse flanges of the pterygoid anteriorly to between the anterior end of each tooth row (figs. 4, 6). The posterior end of the bone is divided along the midline where the parabasisphenoid projects between the two parts. The vomer deepens anteriorly to a point between the posterior end of the tooth rows, and lessens in height anterior to that. It is very thin except at its anterior end, which broadens to meet the premaxillae along the midline. It is overlain dorsally by the medial part of the palatines, and posteriorly it underlies the anterior process of the pterygoid.

BRAINCASE

The bones of the braincase are completely coossified, and sutures are not evident between the supraoccipital, epiotic, exoccipital, opisthotic, prootic, laterosphenoid, basisphenoid, parasphenoid, basioccipital, and, if present, orbitosphenoid (fig. 8). The borders of the individual elements are indicated in a few areas by discontinuities in the surface of the bone, but most contacts are obliterated.

The basisphenoid portion is extremely large and filled with extensive pneumatic spaces (figs. 4, 7, 8). Together these cavities encompass a space larger than the endocranial cavity. The inside of the basisphenoid is exposed, revealing a complex system of struts and cavities very similar to those of protosuchid crocodylomorphs (Busbey and Gow, 1984). A pair of parasagittal septa divide the space into a nearly enclosed space along the midline and a lateral space confluent with the middle ear cavity; the midline space is subdivided by delicate septae and processes (fig. 8).

These spaces presumably communicate with the eustachian tubes, but the precise location of the opening for it is unclear. Eustachian openings in other archosaurs lie bilaterally near the contact between the basioccipital and basisphenoid, but fusion between these two elements obscures this contact in *Erlicosaurus*. Two openings are evident on the right side of the specimen near
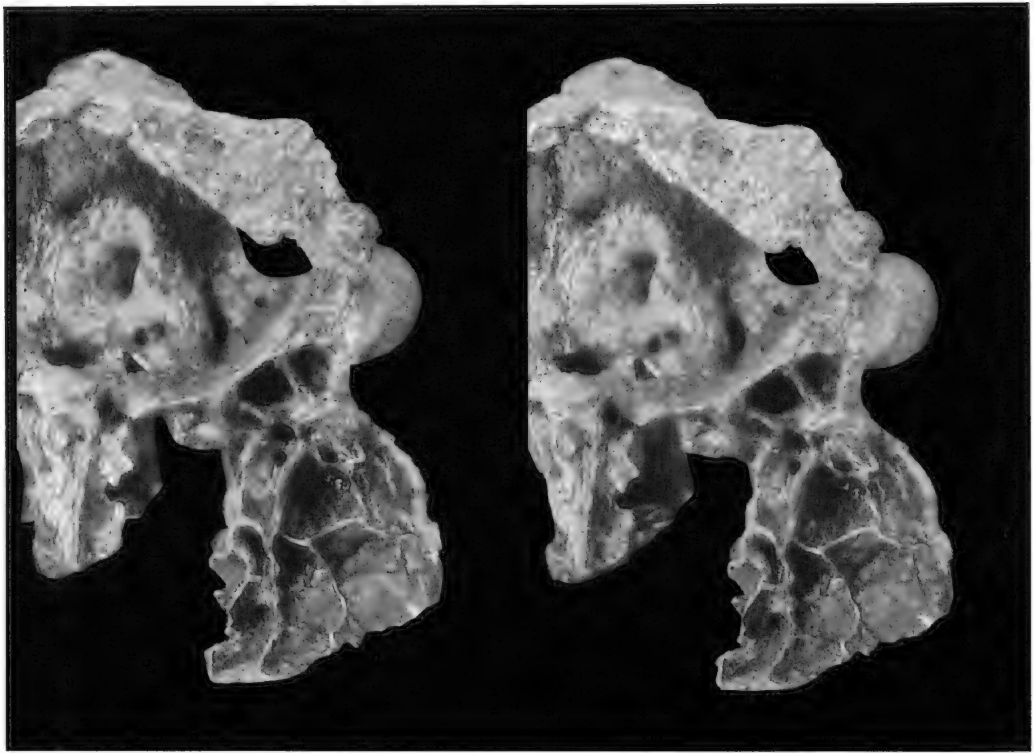
Fig. 8.   Stereophotographs of the right side of the braincase of the *Erlicosaurus andrewsi* holotype in medial view. Abbreviations: de opening for endolymphatic duct; fj jugular foramen; fhyp hypophysial fossa; fm foramen magnum; fs floccular fossa; pn pneumatic pockets within basisphenoid portion of braincase; V trigeminal opening; VII foramen for facial nerve; VIII foramina for statoacoustic nerve; XII hypoglossal foramina.

the presumed contact, but as discussed below the dorsal of the two is inferred to be for the carotid artery within the exoccipital. We therefore tentatively identify the ventral of the two as the eustachian tube (fig. 7). This opening lies in a depression on the posteroventral surface of the basisphenoid near its lateral edge. Unfortunately, it is filled with matrix and its precise course within the braincase cannot be verified. There is no evidence of an opening or depression on the midline at the presumed contact between the basisphenoid and basioccipital.

The spaces within the basisphenoid are separated by delicate struts and septa (fig. 8). Many of these are incomplete or broken, however, and it is not possible to reconstruct all of the connections and separations between the spaces. The remains of a large, parasagittal septum on both sides of the skull indicate that it separated a large central space

from the extensive middle ear cavity. The better preserved septum on the left side is composed of two parts with different orientations that meet obliquely. The posterior part is oriented to face posteroventromedially, and the anterior part faces anteroventromedially. The eustachian tube enters the middle ear cavity immediately lateral to the septum.

The ventral surface of the basisphenoid is extensive, forming a convex expansion beneath the braincase (figs. 4, 7). The basisphenoid descends vertically from its contact with the basioccipital on the occiput and arches anteriorly. An elongate convexity is formed ventrally along the midline. A depression is situated lateral to this convexity, in which the eustachian opening lies.

Well-developed basipterygoid processes are not evident (fig. 6). Irregularities along the anterolateral edge of the braincase posterior to the cultriform process may correspond to
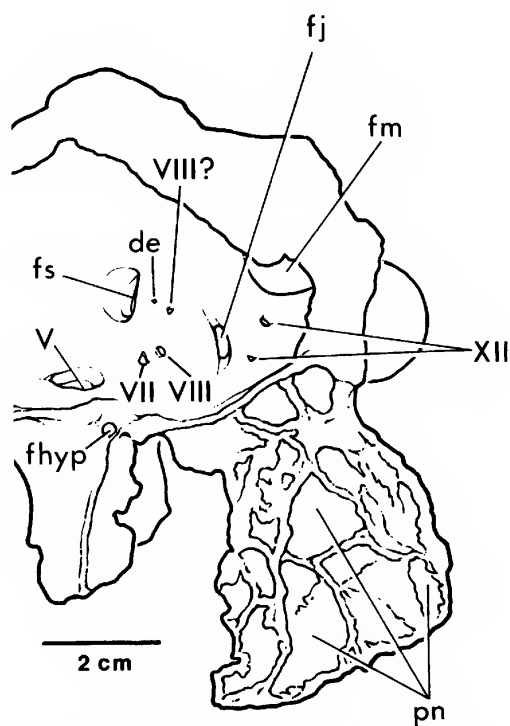
fj

fm

VIII?

de

fs

V

VII VIII

fhyp

XII

pn

2 cm

Fig. 8.   Continued.

to the foramen vagi, slightly dorsal to the level of the contact between the quadrate and the ventrolateral part of the occiput. It leads anteriorly into an osseous passage beneath the fenestra ovale on the medial surface of the middle ear cavity. Its anterior end is incomplete, but it leads to the typical position within the basisphenoid beneath the hypophysial fossa.

The medial surface of the braincase wall is well preserved on the right side (fig. 8). The jugular foramen, a broad vertical slit, is immediately posterior to the vestibular eminence. It exits from the occiput ventrolaterally between the hypoglossal foramen and the posterior carotid foramen. A small foramen is present immediately ventrolateral to the foramen vagi, but its source is unclear. Perhaps it is for the glossopharyngeal (IX) or spinal accessory (XI) nerve, originating within the jugular foramen. A small hypoglossal foramen lies medial to the jugular foramen within the braincase, and a much larger one lies posterior to it. The latter exits immediately lateral to the occipital condyle. The exit of the passage leading from the more anterior hypoglossal foramen probably lies within a depression ventral to the larger hypoglossal foramen and medial to the foramen vagi, preserved only on the right side, but this area has not been completely prepared.

The facial foramen (for cranial nerve VII) and acousticovestibular foramen (for cranial nerve VIII) are closely situated immediately anterior to the base of the vestibular eminence within the endocranial cavity. A division within the acousticovestibular foramen into channels for the cochlear and vestibular branches of cranial nerve VIII is not visible. Two small foramina pierce the vertical component of the vestibular eminence near the lagenar swelling. The anterodorsal of the two is probably the endolymphatic duct, and the posteroventral one a branch of the eighth nerve.

The subarcuate (floccular) fossa anterodorsal to the vestibular eminence is extremely deep. It extends posterolaterally at least into the medial base of the paroccipital process, but its deepest recess has not been exposed. It tapers distally and is higher than wide.

The anterolateral wall of the braincase is

this process, but there is no indication that a synovial joint was present. A parabasal canal may be present in this region (Barsbold, 1983: 15) but could not be verified.

The portion of the basisphenoid flooring the endocranial cavity is damaged along the midline and anteriorly. Although the right side of the sella turcica is well preserved, the hypophysial fossa is incompletely preserved (fig. 8). A large foramen is exposed posterior to the sella turcica, with its medial surface broken away, and is presumably for cranial nerve VI. It passes ventrally, paralleling a groove immediately lateral to it. The preserved portion of the passage for the internal carotid artery on the right side ends posteroventral to the sella turcica, and its anterior continuation is not preserved. The left passage has not been prepared.

The passage for the internal carotid artery leads forward from a foramen on the ventrolateral part of the occiput. The foramen is obscured on the left side but is well delineated on the right side. It is located ventrolateral

poorly preserved on both sides. The latero-sphenoid and/or orbitosphenoid form an anterior floor to the endocranial cavity, but the exits of cranial nerves II, III, and IV are not visible. The cerebral cavity is large, and the laterosphenoid bulges far laterally. The capitate process of the laterosphenoid is vertically oriented and curves anterolaterally to contact the postorbital.

The fenestra ovalis and recessus scalae tympani are not exposed. The area in which they occur, posterior to the lateral opening for cranial nerve VII, is covered by matrix. This area is bounded below by a prominent expansion of bone probably enclosing the inner ear.

Dorsal and slightly posterior to the area of the fenestra ovale, a large opening connects the middle ear cavity with the hollow paroccipital process. This opening, identified as the fenestra pseudorotunda by Perle (1981: fig. 4), probably enclosed a posterior extension of the caudal tympanic recess. The opening is oval, about 1 cm wide and ½ cm high, opening posterodorsally into the anteroventral edge of the paroccipital process. It is separated from the middle ear cavity by a narrow space connected with the supratemporal fossa anteriorly and the occiput posteriorly. The connection with the occiput, in a position similar to the cranioquadrate passage of crocodyliforms, passes between the paroccipital process and the metotic part of the opisthotic medial to the dorsal part of the external auditory meatus. Presumably the temporo-orbital artery passed through this passage, and perhaps, as in crocodylians, the main trunk of the facial nerve passed from the middle ear cavity posteriorly through this passage.

The right paroccipital process is broken distally, showing the process to be entirely hollow (fig. 7). The medialmost recess has not been completely prepared, so it cannot be discerned whether a wall separates this space from the endocranial cavity through the subarcuate fossa.

The paroccipital process is nearly transverse in orientation, its distal end curving posteriorly at an angle of less than 10°. The distal end expands slightly and extends further ventrally than dorsally, as seen on the left side. A broad, well-developed depression lies immediately lateral to the foramen mag-num. Lateral to this depression the process has a convex posterior surface. An opening for the occipital artery is not apparent on the posterior surface of the paroccipital process.

The trigeminal opening is complex. It begins as a single large opening on the ventro-medial surface of the endocranial cavity (fig. 8). The ophthalmic branch of the trigeminal nerve (V1) exits anteriorly from within this opening, and passes a short distance to exit anteriorly from the anteroventral wall of the braincase. Distal to this branch the passage extends laterally and branches into a dorsal passage for the maxillary branch (V2) and a ventral passage for the mandibular branch (V3). These exit laterally onto the posterior wall of the supratemporal fossa and are widely separated (> 1 cm) from the opening for V1.

The middle ear cavity is entirely enclosed by the braincase and quadrate except for a greatly restricted external auditory meatus posterodorsally. The braincase and quadrate form a deep anterolateral wall to the middle ear cavity that narrows anteriorly. The external auditory meatus passes posterior to the dorsal part of the quadrate through an opening less than one-third the height of the quadrate (fig. 7). The orientation of the stapes, as indicated by the inferred position of the fenestra ovalis and the external auditory meatus, is posterodorsolateral, similar to that of most dinosaurs (e.g., *Plateosaurus engelhardti*).

The cultriform process of the parasphenoid is short, slender, and vertically expanded, extending anteriorly from the ventral part of the braincase (fig. 6). It projects along the midline between the posterior division of the vomer. Dorsal to the posterior end of the vomer it is overlain by the anterior blade of the pterygoid; its dorsal part is therefore not exposed on the specimen. It tapers in height anteriorly.

The occipital condyle is nearly hemispherical but is flattened dorsally. A low, indistinct ridge descends from the condyle to the basisphenoid, and a gentle fossa is developed on each side. Well-developed areas for the insertion of axial muscles are absent, although the area near the presumed contact between the basioccipital and basisphenoid is slightly rugose.

Fig. 9.   Stereophotographs of the holotype mandible of *Erlicosaurus andrewsi* in dorsal view.

The supraoccipital area is oriented posterodorsally (fig. 7). It is dominated by a large nuchal crest along the midline, extending from about 1 cm dorsal to the foramen magnum to the dorsal edge of the occiput. The entire dorsal edge of the foramen magnum is rugose. Immediately dorsal to the crest the supraoccipital is incised along the midline, forming with the parietal a small (~5 mm) dorsal opening. A break across the supraoccipital area (fig. 8) demonstrates that the tympanic air spaces did not connect across the midline, as in crocodylians and some birds.

MANDIBLE

Both hemimandibles are preserved, but the right articular and the posterior part of the right surangular are missing (figs. 9, 10). The two hemimandibles are preserved separately, and the surface of each facet for the mandib-

ular symphysis has matrix on it, indicating that the symphyseal suture was weak.

The edentulous symphyseal region of the **dentary** is broad and U-shaped in dorsal view, with a nearly transverse anterior margin. There is no evidence of a predentary bone. The dorsal margin of the edentulous region is sharp, and presumably bore a keratinous structure. The mandibular symphysis is short, extending over slightly more than 1 cm in length. The symphysis faces posterodorsally, and its posterodorsal surface is concave dorsally and convex ventrally. In anterior view, the dorsal edge of the symphysis descends slightly toward the midline. A large foramen opens from the anterior surface of the dentary midway between the symphysis and the lateral edge.

The dorsal edge of the dentary is nearly straight throughout most of its length but bends sharply beneath the fifth tooth so that
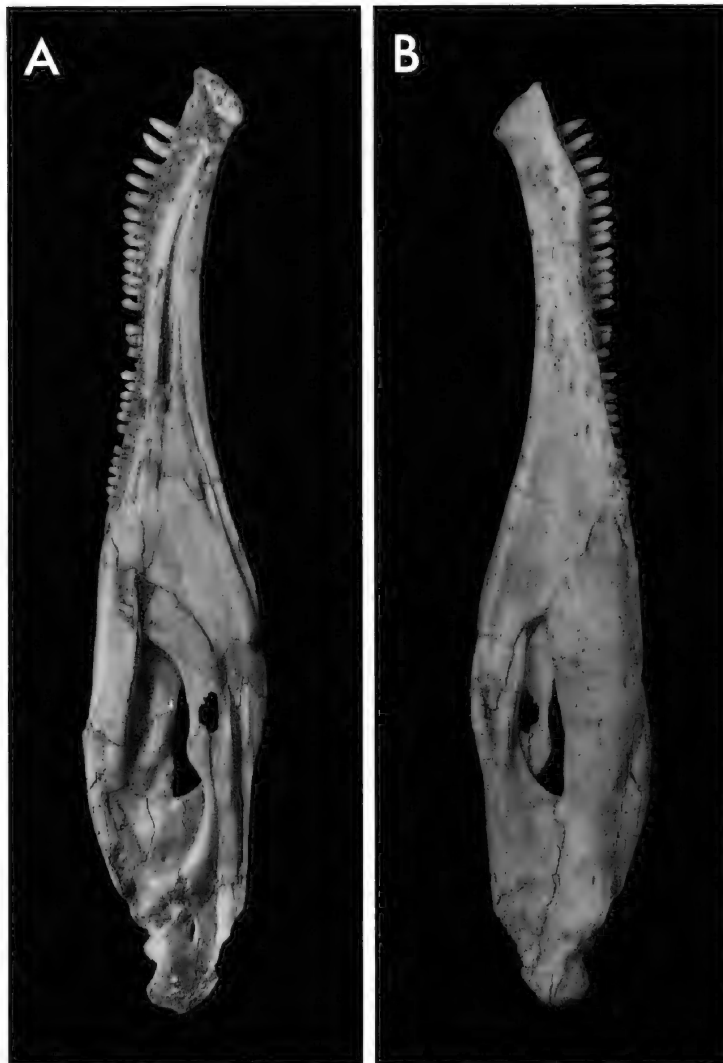
Fig. 10.   Holotype left hemimandible of *Erlicosaurus andrewsi* in lateral (**A**) and medial (**B**) views. Abbreviations: an angular; ct? possible opening for chorda tympani nerve; d dentary; fml lateral mandibular fenestra; pr prearticular; sa surangular; sp splenial.

the anterior part descends anteriorly (fig. 10). Its ventral margin descends posteriorly and at its anterior end, forming a gently concave ventral edge in lateral view. The ventral part of the dentary projects posteriorly beneath the lateral mandibular fenestra into a groove on the lateral surface of the angular. The dorsal part of the dentary does not extend posteriorly dorsal to the fenestra, and instead recedes dorsally. In lateral view, the posterior end of the dentary therefore forms a posterodorsal-facing edge excavated by the anterior end of the lateral mandibular fenestra. Dor-

sally, the surangular divides into two anteriorly projecting processes, one on the posterolateral surface of the dentary, the other on its posterodorsal surface. The dentary sends a short, stout process between this division in the surangular that projects onto the dorsal edge of the surangular. The much greater length of the groove on the surangular that receives this process indicates that the process is incomplete. This contact and the contact with the angular appear very loose, suggesting that a great deal of movement was possible between the dentary and the post-
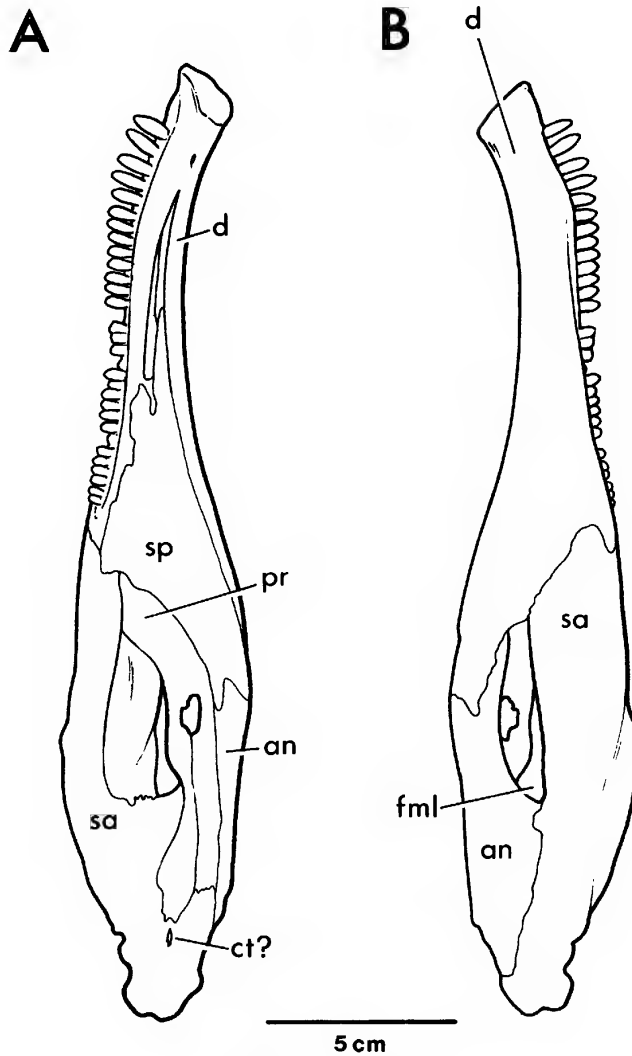
Fig. 10. Continued.

dentary part of the mandible, as in most theropods.

The dorsal margin of the dentary forms a wide, nearly flat surface posterior to the fifth tooth (fig. 9). All of the teeth posterior to the fifth are therefore considerably inset from the margin of the dentary. The surface curves as it passes posteriorly; anteriorly it faces slightly laterally, and posteriorly it comes to face slightly medially. This shelf is continuous posteriorly with the blunt process between the division in the surangular. A large foramen exits posteriorly from this shelf opposite the 21st tooth position.

The Meckelian groove is deeply incised into the medial surface of the dentary but becomes shallower anteriorly until it terminates below the fourth tooth. Posteriorly it is covered by the splenial, but it apparently broadens to become confluent with the mandibular fossa. Its anterior end is closer to the ventral edge than the dorsal, but it rises to a level two-thirds the height of the dentary beneath the middle of the tooth row. A small (~2 mm) foramen pierces the posterolateral surface of the symphysis shortly beyond the anterior end of the groove.

Many small foramina pierce the lateral sur-

face of the dentary. In addition to the large foramen on the anterior surface of the symphysis, at least eight tiny foramina are scattered over this surface. Three medium size foramina are aligned longitudinally beneath the second to fourth teeth. Posterior to these foramina, at least seven tiny foramina open into long, narrow grooves extending posteriorly across the surface of the dentary. The longest of these grooves, on the right dentary, is over 2 cm long. No foramina occur in the posteroventral part of the dentary's lateral surface.

The **surangular** forms the dorsal half of the posterior part of the mandible (figs. 9, 10). Its dorsal edge is flat anteriorly and descends posteriorly lateral to the articular. Laterally, it forms a deep flange dorsal to the lateral mandibular fenestra, and is nearly twice as deep as the angular. Anteriorly, the surangular ascends the posterodorsal edge of the dentary and divides into two processes overlapping the dentary. One process overlies the lateral surface of the dentary immediately ventral to the lateral shelf. The second is shorter and much stouter and overlies the posterior end of the shelf on the dorsal surface of the dentary. The dorsal part of the surangular arches over the anterior half of the mandibular adductor fossa, but posteriorly it does not roof the fossa. Ventral to the roof over the anterior part of the fossa, the medial surface of the surangular swells, forming the ventral border to a shallow fossa on the medial surface of the bone.

The posterior part of the surangular broadens and contacts the anterior surface of the articular. The dorsal surface of the surangular forms a deep groove anterior and parallel to the glenoid fossa, bordered posteriorly by the anterior buttress of the glenoid. A small (1 mm) foramen pierces the lateral surface of the surangular lateral to this posterior broadening and apparently passes through it to exit on the medial surface. It is in the same position as the larger foramen typical of carnosaurian theropods. A similar size foramen exits anteriorly from the lateral surface of the surangular two-thirds of the way anteriorly. In the region anterior to this foramen the two surangulars exhibit different patterns of vascular openings. On the left side, a deep longitudinal groove near the dorsal edge is incompletely closed dorsolaterally. It nearly

closes twice, and is completely open posteriorly and anteriorly. On the right side, two tiny foramina exit into long grooves on the dorsolateral surface. Anterior to these foramina a larger opening, apparently comparable to that on the left side, enters the posterior end of the groove for the posterior process of the dentary. Posteriorly, the surangular overlies the articular and forms the lateral border of the glenoid fossa. It extends posteriorly nearly to the end of the mandible.

The **angular** forms the ventral part of the posterior end of the mandible (figs. 9, 10). It forms the ventral border of the lateral mandibular fenestra, and posterior to the fenestra it expands dorsally. Anteriorly, it articulates with the posteroventral part of the dentary and splenial. The dentary articulates with a broad, shallow groove on the angular, whereas the posteriorly divided splenial overlies a ridge on the angular. Both joints appear to have allowed a large degree of movement. Dorsally, the surangular contacts the angular over about half its length. Posteriorly, the angular underlies the articular and extends nearly to the end of the mandible.

The **splenial** is a thin, triangular bone covering the medial surface of the posterior part of the dentary (fig. 10). Its ventral edge follows the ventral edge of the hemimandible as it ascends anteriorly, and its dorsal edge follows the dorsal edge of the dentary opposite the posterior part of the tooth row. Its posterior edge is gently concave and covered by the prearticular medially. The dorsal part of the splenial overlies the medial surface of the dentary and anteriormost surangular, but the ventral part of the splenial overlies the dentary dorsally within the broadened Meckelian groove. The splenial tapers anteriorly, and abruptly narrows beneath the 20th tooth position, due to the descent of the dorsal edge. A large (~6 mm long, 2 mm high) foramen opens posteriorly from the middle of the ventral edge. A smaller foramen is partially enclosed by the dorsal edge of the splenial near the posterior end of the tooth row. The posteroventral end of the splenial is forked and overlies a strong ridge on the medial surface of the angular. The posterodorsal fork enters into a groove between this ridge and the prearticular bone, extending onto the ventromedial surface of the angular.

The left **articular** is complete and well pre-

served (figs. 9–11). It is less massive than in most dinosaurs, and is similar in thickness to bones such as the surangular. The glenoid fossa is situated below the level of the mandibular tooth row, at about the middle of the vertical extent of the mandible. The fossa is oriented obliquely at approximately 45°, mirroring the posterolateral direction of the quadrate condyle. The glenoid is buttressed by a stout process anterolaterally and another posteromedially, and it is narrowest between these processes. The anterolateral process is convex along the margin of the fossa, the posteromedial process concave. Because of slight distortion to the quadrate and articular, it is unclear whether the middle of the three condyles on the quadrate articulates with this posteromedial buttress; it appears to articulate medial to it. The middle of the three condyles on the quadrate does not appear to articulate with the articular.

The anterolateral buttress to the glenoid fossa was identified as an anterior articular bone (similar to that identified by Madsen [1976] in *Allosaurus fragilis*) by Perle (1981). It is unclear whether this bone is indeed a separate ossification, however.

A small (~1–2 mm) foramen posterior to the glenoid on the lateral edge of the posteromedial buttress is probably the foramen aërum (fig. 11). It is in the same position as the foramen aërum of birds and crocodylians, and it is further lateral than would be expected of an opening for the chorda tympani nerve.

The retroarticular process is deeply concave dorsally, forming a groove parallel to the glenoid fossa. In anteromedial view, this gives the articular a W-shaped outline. The fossa on the retroarticular process is higher medially than laterally, sloping posterolaterally. The posteromedial edge of the retroarticular process is upturned, forming a blunt, vertical process about as high as the processes buttressing the glenoid. The ventral edge of the retroarticular process forms a sharp ridge curving smoothly downward anteriorly.

The articular forms the dorsal border of a small (~3 mm long, 1 mm high) foramen medially beneath the glenoid. The ventral border is formed by the prearticular. A small passage leads posteriorly from the foramen, and a larger passage leads anteriorly into the mandibular adductor fossa, possibly for the
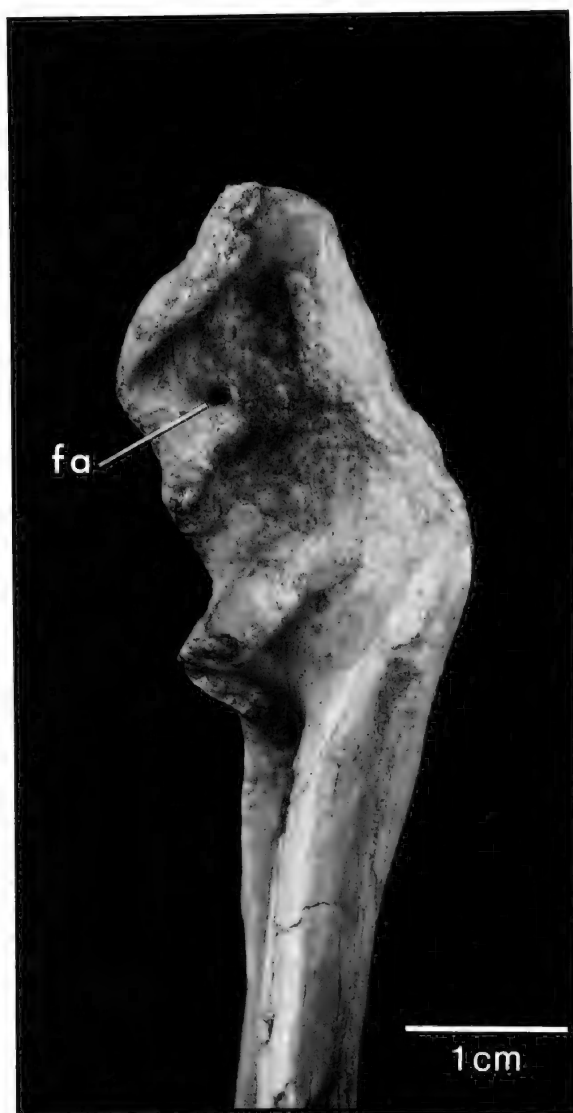

Fig. 11. Articular region of the holotype left hemimandible of *Erlicosaurus andrewsi* in dorsal view. Abbreviation: fa foramen aërum.

chorda tympani branch of the facial nerve. The articulations of the articular with the angular and surangular are unclear.

The **prearticular** is a crescentic band of bone forming a ventromedial wall to the mandibular adductor fossa (fig. 10). Its posterior end articulates with the medial surface of the articular, extending posteriorly nearly to the end of the mandible. A dorsal process ascends along the medial surface of the anterior buttress of the glenoid. Anterior to the articular the dorsal edge of the prearticular curls

Fig. 12. Scanning electron micrographs of the 19th dentary tooth of the holotype left hemimandible of *Erlicosaurus andrewsi* in **(A)** medial, **(B)** lateral, and **(C)** posterior views. Magnification ×20; differences in apparent size are due to foreshortening caused by slightly different orientations.

laterally, forming a brief roof to the posterior end of the adductor fossa. A blunt dorsal process interrupts the dorsal curvature of the prearticular in the middle of the adductor fossa. The ventral edge of the prearticular curls laterally below this blunt process, covering the dorsal edge of the angular. Anteriorly, the prearticular contacts the posterodorsal edge of the splenial and continues dorsally to contact the surangular. There is no evidence for an internal mandibular fenestra (foramen intermandibularis caudalis of crocodylians) between these two bones. An opening in the middle of the left prearticular is due to breakage, as indicated by its absence from the right element.

A **coronoid** is absent. The dorsal part of the left and right splenial are cracked in the area a suture might be expected, but in both cases there is no indication of overlap between the bone on the two sides of the crack, and close inspection reveals clear signs of breakage. There is, furthermore, no indication of an articulation for a coronoid on the medial surface of the splenial and dentary.

DENTITION

The dentition comprises 23 tooth positions in the maxilla and 31 tooth positions in the dentary. The additional teeth in the dentary are anteriorly placed, opposite the edentulous premaxilla.

The maxillary teeth are nearly homodont and are similar to all but the anteriormost dentary teeth (figs. 1, 2, 4, 5). They are transversely compressed, and in lateral view they are lanceolate, nearly symmetrical (but the posterior edge is slightly more extensive than the anterior), with a rounded apex and slightly convex anterior and posterior edges. These edges are denticulated. The bases of the maxillary teeth are constricted slightly.

The denticles on the anterior and posterior edges are proportionately larger than in most theropod teeth. On the dentary tooth in figure 12, the basal denticle length is 0.21 mm on both anterior and posterior edges and the fore–aft basal length of the tooth is 2.05 mm. This basal denticle length is outside the 95% confidence intervals calculated by Farlow et al. (1991) for a sample of theropods (excluding two outlying taxa); using their regression analyses (pp. 167–170), the basal denticle length should be between 0.155 and 0.158 mm on the anterior edge and between 0.18 and 0.19 mm on the posterior edge for a tooth of this fore–aft basal length.

The anterior maxillary teeth are oriented

vertically, but posteriorly they become more ventrolaterally oriented. This occurs to a similar degree on both sides of the skull, so that the posteriormost teeth are oriented at nearly 45°. Although this does not appear to be distorted, the lack of a similar orientation to the posterior dentary teeth suggests that distortion may nevertheless be responsible.

The anterior dentary teeth are nearly conical, but posteriorly they gradually become more lanceolate (fig. 10). These anterior teeth curve slightly dorsolaterally and are not constricted at their bases. They are taller than the posterior teeth, the tallest having about twice as much exposure above the dentary as the posterior teeth.

Tooth implantation is thecodont, and all teeth are separated by septa. The roots of all teeth are nearly circular in cross section. The interalveolar septa are exposed as interdental plates on the medial surface of the anterior part of the dentary and the medial surface of the posterior part of the maxilla (fig. 6). Most teeth are appressed to the lateral surface of the alveoli, but the anteriormost five or six teeth in the maxilla and dentary are centrally placed within the alveoli. There is no evidence of tooth-to-tooth wear.

Only a few teeth are in the process of replacement, although matrix may obscure some of them. Replacement takes place along the medial surface of the tooth being replaced. In the most complete tooth row—the lower left—the anterior 13 teeth are all fully erupted, but the tips of replacement teeth are emerging beneath the 8th and 12th. The 14th is absent, the 15th fully erupted, and the 16th is in the process of replacement, with the old tooth nearly shed. The 17th and 19th are erupted, the 18th is emerging in an empty alveolus, the 20th is nearly fully erupted, and no replacement teeth are evident in the remaining positions.

DISCUSSION

The cranial structure of *Erlicosaurus andrewsi* presents a remarkable combination of unique features and features shared with other dinosaurian taxa only distantly related to one another. Because of this, and because the postcranial skeleton of "segnosaurs" (represented by most elements except for those of the forearm, carpus, and manus) presents a similar chimera, their relationships have been unclear. The recently described taxon *Alxasaurus elesitaiensis* is important in combining a forelimb similar to that of *Therizinosaurus cheloniformis* with a mandible, vertebral column, pelvis, and hindlimb similar to that of "segnosaurs," demonstrating a close relationship between the three taxa (Russell and Dong, 1993). Furthermore, the theropod features of the forelimb of *Alxasaurus elesitaiensis* and *Therizinosaurus cheloniformis* offer substantial evidence that the group as a whole is a member of Theropoda (Russell and Dong, 1993).

We are currently studying the relationships of maniraptoran theropods based on new material from the Late Cretaceous of Mongolia. Because we have not yet examined material of several critical taxa, we do not present a detailed analysis of Maniraptora here. Instead, we present our observations on cranial features within the context of the analyses of theropod relationships by Gauthier (1986) and others. We will first discuss the cranial features of *Erlicosaurus andrewsi* in reference to those recognized as apomorphic for Saurischia and groups within it in recent analyses; then we will comment briefly on previous hypotheses of relationship of therizinosauroids outside Theropoda.

The major phylogenetic conclusions of Gauthier (1986) are presented in figure 13. Much information relevant to theropod relationships has come to light subsequent to publication of this paper, but a detailed, comprehensive reanalysis based on direct examination of fossil material remains to be published.

The most comprehensive analysis of Theropoda subsequent to that of Gauthier was recently published by Holtz (1994). Although this analysis improves on that of Gauthier, especially in its consideration of size-related characters and the larger number of taxa and characters analyzed, we disagree with its treatment of several characters. For example, our examination of specimens and the literature does not support the coding of several characters (e.g., Holtz's character 38 for Dromaeosauridae, characters 81, 99, and 114 for *Archaeopteryx,* character 114 for *Ornitholestes,* characters 89 and 119 for Ornithomimosauria). Furthermore, the lack of specifi-
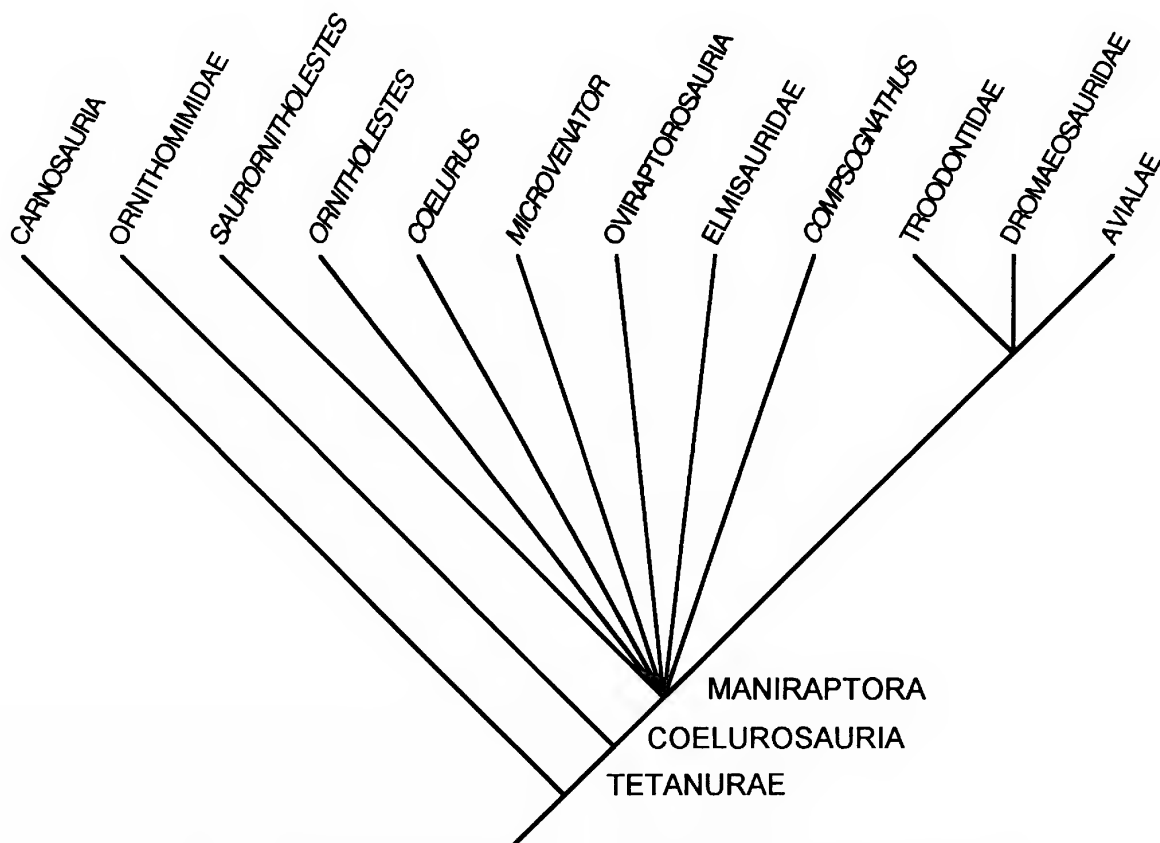
Fig. 13. Relationships among Theropoda hypothesized by Gauthier (1986).

cation of the primitive condition for each character leads to potential redundancy between some (e.g., 52 and 72), and the extreme brevity of the character descriptions renders several of them confusing and difficult to distinguish (e.g., characters 64—"large depression in the periotic region;" 69—"large excavation around the fenestra ovalis;" and 115—"periotic region highly pneumatized"). For these reasons we are skeptical of the main conclusion of Holtz's analysis—that Tyrannosauridae are members of Maniraptora—although the evidence Holtz presents for inclusion of Ornithomimosauria within Maniraptora and for *Elaphrosaurus* and Abelisauridae within Ceratosauria is more convincing.

Russell and Dong (1993) presented a cladistic analysis of selected tetanuran Theropoda in their description of *Alxasaurus elesitaiensis,* and the most parsimonious cladogram has several novel features. In particular, it

places dromaeosaurs as the sister group of tyrannosaurs within Carnosauria. However, for reasons not discussed in the text, many characters (e.g., the synapomorphies of Maniraptora) and taxa (e.g., Avialae) included by Gauthier (1986) were not considered. Our examination of the skull of *Erlicosaurus andrewsi* (which Russell and Dong were unable to examine) does not support the coding of their characters 9 and 13 for Therizinosauridae, and to our knowledge the vomer of oviraptorosaurs does not extend further posteriorly than in other Tetanurae (character 12). Although the analyses of Gauthier and Holtz did not consider Therizinosauroidea, the larger number of taxa and characters considered by both strongly suggests that the different results of the analysis of Russell and Dong are due to the particular characters included in their analysis rather than inclusion of Therizinosauridae.

Less comprehensive, but more detailed

work on a taxon hypothesized to be a basal member of Theropoda was recently presented by Novas and Sereno (Novas, 1994; Sereno, 1994; Sereno and Novas, 1994). *Herrerasaurus ischigualastensis* Reig, 1963, combines features previously interpreted as plesiomorphic for Dinosauria with some interpreted as apomorphic for Theropoda. Novas and Sereno argued that the weight of the evidence favors a relationship within Theropoda. An even more plesiomorphic taxon *Eoraptor lunensis* Sereno et al., 1993, has been given a brief description, and the authors hypothesized that it is the most basal member of the Theropoda.

THE SKULL AND MANDIBLE OF *ERLICOSAURUS ANDREWSI* AND APOMORPHIES OF SAURISCHIAN CLADES

In this section we discuss the skull and mandibular characters of *Erlicosaurus andrewsi* in the context of the synapomorphy schemes of several recent analyses of relationships among Saurischia. *Erlicosaurus andrewsi* lacks most features diagnosing the Sauropodomorpha (Gauthier, 1986), Ceratosauria (Gauthier, 1986; Rowe and Gauthier, 1990; Holtz, 1994), and Carnosauria (Gauthier, 1986; Molnar et al., 1990), including their constituent taxa, and these groups are not discussed below except where noted.

SAURISCHIA

Three features are considered to be synapomorphies of Saurischia by Sereno et al. (1993), Novas (1994), and Sereno and Novas (1994). The condition in the immediate outgroups to Dinosauria is unknown for all three features, but the primitive condition is present in more distant outgroups and in Ornithischia.

Subnarial foramen—The presence of a small foramen between the premaxilla and maxilla is hypothesized to be a synapomorphy of Saurischia. In *Erlicosaurus andrewsi* this region is only preserved on the right side of the skull (fig. 3), and a matrix-filled area may correspond to this feature but requires further preparation.

Jugal posterior process forked—Primitively, the posterior process of the jugal in Saurischia is forked in lateral view, with an an-

terior process of the quadratojugal extending between the prongs, suggestive of movement between the two bones. This is the condition in *Erlicosaurus andrewsi* (fig. 1).

Jugal overlaps laterally onto lacrimal—The contact between the jugal and lacrimal differs slightly among primitive Ornithischia and more distant outgroups to Saurischia, but all lack the broad overlap of the lacrimal by the jugal. This condition is present in *Erlicosaurus andrewsi* (fig. 1).

THEROPODA

With the inclusion of *Eoraptor lunensis* within Theropoda, Sereno et al. (1993) and Novas (1994) identified no cranial synapomorphies of Theropoda. The unnamed clade comprising Herrerasauridae and Theropoda other than *Erlicosaurus lunensis* was diagnosed by Sereno et al. (1993), Novas (1994), and Sereno and Novas (1994) by a suite of characters including the following:

Intramandibular joint—In most Theropoda a complex joint is present between the surangular and dentary dorsolaterally, the splenial and angular ventromedially, and, to a lesser extent, the dentary and angular ventrolaterally (Gauthier, 1986; Sereno and Novas, 1994). This joint is well developed in *Erlicosaurus andrewsi* (fig. 10).

The clade comprising the Ceratosauria and Tetanurae of Gauthier and excluding *Eoraptor lunensis* and Herrerasauridae, a clade previously equivalent to the Theropoda, is diagnosed by the following cranial features:

Interdental plates—The presence of medial expansions of the septa separating teeth, and their exposure medially on the dentary, premaxilla, and maxilla, thus far has only been recognized in Theropoda. The condition in *Eoraptor lunensis* and Herrerasauridae is not described in the literature, although it appears that the herrerasaurid *Staurikosaurus pricei* Colbert, 1970, lacks this feature. Interdental plates are present in *Erlicosaurus andrewsi* (figs. 6, 10); although the plates are absent or fused in troodontids (Currie, 1987b) and most basal Avialae, they are present in most other Maniraptora (including *Archaeopteryx lithographica*; Wellnhofer, 1994).

Accessory antorbital (maxillary) fenes-

tra—The presence of one or more small fenestrae in the medial wall of the antorbital fossa has long been considered a synapomorphy of Theropoda. The near absence of the medial wall of the fossa in *Herrerasaurus ischigualastensis* suggests that the absence of an accessory fenestra may be related to this autapomorphic condition, and, more to the point, it is not possible to assess whether a fenestra is present when there is no bone where one is to be expected. The level at which this fenestra is an apomorphy, either at this clade or at the clade comprising Herrerasauridae and this clade, is therefore ambiguous. Otherwise, an accessory fenestra is present in all known Theropoda except birds more derived than *Archaeopteryx lithographica*. In any case, the apparent absence of accessory fenestrae in *Erlicosaurus andrewsi* (figs. 1, 2, 5) is discordant with other features placing it in Maniraptora but outside Avialae. It is possible that one or two small fenestrae are present but unrecognized in areas not fully prepared on the skull, but if so they are unusually small.

TETANURAE

Absence of enlarged fanglike anterior dentary tooth—Gauthier (1986) noted that in basal Dinosauria and Ceratosauria a fanglike tooth is present in the anterior part of the dentary opposite the contact between the premaxilla and maxilla. In *Herrerasaurus ischigualastensis* the third and fourth teeth in the dentary are the largest, although the difference in size is small. In *Erlicosaurus andrewsi,* although the lower teeth increase in size anteriorly, the teeth opposite the contact between the premaxilla and maxilla are no larger than their neighbors (fig. 10).

Accessory-antorbital (maxillary) fenestra large and posteriorly placed—As discussed above, *Erlicosaurus andrewsi* apparently lacks an accessory antorbital fenestra.

Antorbital tooth row—In all Tetanurae the tooth row ends anterior to the orbit (Gauthier, 1986), unlike in Ceratosauria, *Herrerasaurus ischigualastensis,* and *Eoraptor lunensis.* This is the condition in *Erlicosaurus andrewsi* (figs. 1, 2).

Reduced rim around antorbital fossa—In Theropoda, primitively, the antorbital fossa is surrounded by a well-developed rim. This

rim is reduced to a variable degree in Tetanurae. The antorbital fossa of *Erlicosaurus andrewsi* has a well-developed rim (fig. 5), more extensive than in any other theropod and similar to that of basal Sauropodomorpha.

Caudal (posterior) tympanic recess—An opening into the anterior surface of the paroccipital process is present in all birds and in several basal tetanurans, although the condition in more basal theropods is uncertain and a similar feature is present in Crocodylomorpha (Witmer, 1990). This feature is well developed in *Erlicosaurus andrewsi.*

MANIRAPTORA AND COELUROSAURIA

Gauthier (1986) recognized a clade of long-armed Theropoda including Ornithomimosauria and a diverse array of taxa including Oviraptorosauria, Troodontidae, Dromaeosauridae, and birds (Avialae). He redefined the taxon Coelurosauria as the name-bearer of this clade, and proposed that the Ornithomimosauria comprise the sister group of the clade Maniraptora. Subsequently, Holtz (in press) presented evidence that the Ornithomimosauria are members of Maniraptora (i.e., are more closely related to birds than are some of the taxa included by Gauthier within Maniraptora). We are currently involved in a more detailed examination of the relationships among these taxa and defer treatment of the question of ornithomimosaurian relationships to a later date.

Subsidiary fenestra between pterygoid and palatine—The presence of a fenestra between the pterygoid and palatine on the palate was recognized by Gauthier (1986: 26) as a synapomorphy of Coelurosauria that is modified in birds. Although a fenestra in the skull of *Erlicosaurus andrewsi* is not visible in ventral view, its presence is indicated by the incised medial edge of the palatine as seen in dorsolateral view (figs. 1, 5).

Deeply excavated pocket on ventral surface of ectopterygoid—The presence of this distinctive pocket cannot be ascertained in *Erlicosaurus andrewsi* because this part of the ectopterygoid is not preserved on either side of the skull (fig. 6).

Prefrontal reduced or absent—The absence or reduction of the prefrontal was considered by Gauthier to diagnose the Maniraptora, as

it is not reduced in Ornithomimosauria from the primitive theropod condition. The prefrontal of *Erlicosaurus andrewsi* (fig. 3) is smaller than in Ornithomimosauria and in basal Tetanurae, although it is not as reduced as in most Maniraptora, which have the lacrimal expanded dorsally into the region previously occupied by the prefrontal. The postmortem dislocation of the lacrimals medially on the skull of *Erlicosaurus andrewsi* (figs. 1, 2) obscures the extent to which they are expanded dorsally, but they appear less expanded than in basal Maniraptora.

Enlarged endocranial cavity — The large brain size of extant birds relative to brain size in other sauropsids is reflected in a larger size of the endocranial cavity (Hopson, 1979). Quantitative study of the endocranial cavity of fossil theropods is possible for few specimens, but it is known that the endocranial volume of members of Troodontidae and Ornithomimosauria is larger than in other Dinosauria (Hopson, 1979). Although quantitative assessment of endocranial volume is not possible in many taxa, the ventral surface of the frontals and parietal preserves an impression reflecting the size of the cerebrum. In comparison with other Theropoda, this impression is larger in *Erlicosaurus andrewsi* than in basal taxa such as *Plateosaurus engelhardti*, but similar in size to that of *Troodon formosus* and *Velociraptor mongoliensis*.

Jugal borders antorbital fenestra — Holtz (in press) noted that in Maniraptora, *Dilophosaurus wetherilli*, and tyrannosaurids the jugal extends anteriorly to form part of the border of the antorbital fenestra. This is the condition in *Erlicosaurus andrewsi*.

DROMAEOSAURIDAE AND AVIALAE

Although the pelvis of therizinosaurids is similar to that of dromaeosaurids and Avialae (Barsbold, 1979), the skull of *Erlicosaurus andrewsi* lacks the synapomorphies shared by Dromaeosauridae and Avialae, and those diagnosing each taxon. It does possess a few features in common with taxa within Avialae, but most of these are clearly homoplasies. Among these are the edentulous premaxilla and the fusion of the braincase bones, although the unfused braincase in other Theropoda may be an artifact of sampling non-

terminal ontogenetic stages. The braincase of dromaeosaurids and Avialae may share some of the pneumatic features of *Erlicosaurus andrewsi*, but this region is poorly known in most dromaeosaurids and basal avialians. A foramen aërum is present in the articulars of *Erlicosaurus andrewsi*, Aves, and tyrannosaurids, as well as in many crocodylomorphs (Witmer, 1990), but its distribution among Theropoda is poorly delineated.

ORNITHOMIMOSAURIA, OVIRAPTOROSAURIA, AND TROODONTIDAE

Erlicosaurus andrewsi and some other therizinosauroids share some features with each of these three clades of Maniraptora, and others with two or all three clades.

Numerous, small teeth — The teeth of most theropods are large. In Troodontidae and *Erlicosaurus andrewsi*, *Alxasaurus elesitaiensis*, and *Segnosaurus galbinensis* the teeth are both smaller and more numerous than in other toothed Theropoda. The only ornithomimosaurian with teeth is *Harpymimus okladnikovi*, in which there are only six small teeth restricted to the anterior end of the dentary.

Denticles on teeth large — In their study of tooth serrations in Theropoda, Farlow et al. (1991) demonstrated that serrations on the teeth of Troodontidae are significantly larger than in other Theropoda. As discussed above, those on the teeth of *Erlicosaurus andrewsi* are similarly large, although the form of the teeth is different (fig. 12). The teeth of other therizinosauroids bear even coarser serrations (Russell and Dong, 1993).

Expanded basisphenoid — Troodontidae and Ornithomimosauria both possess an enlargement of the parabasisphenoid that presumably contained pneumatic spaces associated with the eustachian tubes. Although the parasphenoid region is not enlarged in *Erlicosaurus andrewsi*, the basisphenoid is distinctly enlarged (figs. 6, 8), as in these taxa but unlike other nonavialian theropods.

Edentulous premaxilla — An edentulous premaxilla is present in Ornithomimosauria and Oviraptorosauria (as well as in Aves).

Reduced basipterygoid processes, and broad pterygoid closely appressed to braincase — The Oviraptorosauria share with *Erlicosaurus andrewsi* a suite of features related to the basi-

pterygoid articulation that may be two separate characters. In both taxa the basipterygoid process of the basisphenoid is greatly reduced or absent (Russell and Dong, 1993). This brings the quadrate ramus of the pterygoid directly against the lateral surface of the basisphenoid throughout most of its length (fig. 6). The quadrate ramus is also unusually broad in both of these taxa; this may be related to the other modifications, or may be an independent character.

Lateral depression in otic region — The otic region of *Erlicosaurus andrewsi* is surrounded anteriorly, anterodorsally, and anteroventrally by depressions on the lateral surface of the braincase. As noted by Barsbold (1983: 19) this region is similar in a general way to the structure in Troodontidae which he termed the lateral depression (see also Currie, 1985). The condition in *Erlicosaurus andrewsi* is much more extreme, however.

Broad, rounded premaxilla with large palatal shelf — In most basal Theropoda the premaxillae are closely appressed, so that together they are longer than the end of the rostrum is long and form a sharp anterior end to the rostrum. In Oviraptorosauria and Ornithomimosauria the premaxillae are broader than long and in ventral view form a gently rounded anterior end to the rostrum. Furthermore, in all three taxa the premaxilla and the anterior end of the maxilla have a broad palatal portion forming a secondary palate along with the anterior end of the vomer.

Supratemporal fossa does not extend onto posterior edge of frontal — Primitively, in Dinosauria the temporal musculature extends onto the posterior edge of the frontal (Gauthier, 1986; Sereno, 1991). In *Erlicosaurus andrewsi* and at least some Ornithomimosauria (Barsbold and Osmólska, 1990) the frontal also lacks a depression for this musculature, as does the frontal of most Avialae (the condition in *Archaeopteryx lithographica* is indistinct).

Downturned mandibular symphysis — As in *Erlicosaurus andrewsi* (fig. 10), *Alxasaurus elesitaiensis,* and *Segnosaurus galbinensis,* the mandibular symphysis of most Ornithomimosauria, including the primitive taxon *Harpymimus okladnikovi,* is downturned. This condition is not present in any other nonavian Theropoda.

Coronoid absent — A coronoid is present in the mandible of those basal Theropoda for which the mandible is known. This element is reported to be absent in Ornithomimosauria (Barsbold and Osmólska, 1990) and Oviraptorosauria (Barsbold, 1983), as in *Erlicosaurus andrewsi* (fig. 10; Russell and Dong, 1993). It is also absent in extant birds, but the condition in most basal avialians is not clear. Furthermore, although a coronoid is present in *Dromaeosaurus albertensis* (Colbert and Russell, 1969), the condition in other Dromaeosauridae and in Troodontidae is not clear.

In addition to the features just mentioned, the bones of the skull and mandible of *Erlicosaurus andrewsi* are unusually thin and delicate, and those of Troodontidae and Oviraptorosauria are similarly thin and delicate. This feature is difficult to assess, however, and this difficulty is compounded by allometric changes in bone thickness. Also, the maxilla forms the posterior border of the nares in *Erlicosaurus andrewsi* and in Troodontidae, but in *Erlicosaurus andrewsi* this is due to the large size of the nares, whereas in Troodontidae it is due to the small size of the premaxilla. Finally, if Barsbold (1983) is correct in his identification of a parabasal canal in the basisphenoid in *Erlicosaurus andrewsi,* then it shares this feature with Troodontidae and Ornithomimosauria.

THE ORNITHISCHIAN HYPOTHESIS

Paul (1984) presented a "short version" of a "cladistic analysis" (p. 512) involving six dinosaur taxa, and he concluded that segnosaurs (i.e, Therizinosauridae) are the sister group of Ornithischia. He further concluded that prosauropods are the sister group of the group comprising segnosaurs and Ornithischia, so that Saurischia are not monophyletic.

There are numerous problems with the analysis of Paul (1984) that render its results suspect, but insufficient details are presented to evaluate the analysis critically. There is no explanation of how the cladogram was rooted and how characters were optimized, and no tree length statistics are presented. More to the point, a data matrix is not given, so the distribution of characters among taxa cannot be evaluated. Furthermore, it is unclear

whether Paul benefited from examination of actual specimens, and several features of *Erlicosaurus andrewsi* are misrepresented (see below). The monophyly of the basic taxa is not established, and at least one ("early dinosaurs—lagosuchids, lewisuchids, staurikosaurs, herrerasaurs") is not monophyletic. Character descriptions are so brief as to be vague, and some comparisons are of doubtful validity (e.g., the opisthopubic pelvis of some theropods [including birds] is considered comparable with that of ornithischians; the antorbital fossa of ornithischians is considered to be as deeply recessed as in *Erlicosaurus andrewsi* and prosauropods). Other problems with the results presented by Paul are the absence of any synapomorphies for the clade comprising euparkeriids and aetosaurs and the presence of a possible synapomorphy contradicting this arrangement (character 12), the curiously unresolved trichotomy between "early dinosaurs," theropods, and the prosauropod-ornithischian-segnosaur clade, and minor mistakes such as the listing of character 4 twice as a synapomorphy of prosauropods with segnosaurs and ornithischians and the listing of two characters (23 and 34) as possible synapomorphies of segnosaurs and velociraptorines (fig. 5B2) that are then reversed in segnosaurs. Regarding the theropod relationships of segnosaurs, Paul stated that "segnosaurs share no derived characters with theropods that they do not also share with other dinosaurs" (p. 512), but his cladogram shows two such characters (21 and 41).

Of the eight characters listed by Paul supporting a sister-group relationship between ornithischians and segnosaurs, four ("beaked," "post temporal fenestra closed," "opisthopubic pelvis," "lateral malleolus of tibia backs fibula") are also present in theropods. One ("diastema present"), by which Paul apparently means an edentulous region anterior to the tooth row, is open to a different interpretation insofar as it is one state in the transformation series culminating in the absence of a lower dentition, as in Oviraptorosauria and most Ornithomimosauria.

Three characters are supposedly unique to the segnosaur-Ornithischia group: "vomer-pterygoid articulation and the palatine sited posteriorly," "cheeks fully developed," and "main body of astragalus reduced, tibia forms part of articular surface for pes." The first of these may be valid, but the second may be absent in basal Ornithischia and the third definitely is; because therizinosauroids lack all of the diagnostic features of Ornithischia (Sereno, 1986), and are therefore at best their sister group, characters shared only with derived ornithischians must be either ambiguous or homoplasious.

The vomer in primitive ornithischians such as *Lesothosaurus diagnosticus* Galton, 1978, does extend further posteriorly than in most theropods (Sereno, 1991), although not as far posteriorly as in *Erlicosaurus andrewsi*. However, the vomer of some theropods, such as *Allosaurus fragilis,* is nearly as long as in *Lesothosaurus diagnosticus* (see Madsen, 1976). The presence of cheeks is problematic in that cheeks, as indicated by teeth being inset from the skull margin and reduction in number of vascular foramina on the lateral surface of the maxilla and mandible, may not be present in the primitive ornithischian *Lesothosaurus diagnosticus* (see Sereno, 1991), although they are apparently present in *Pisanosaurus mertii* Casamiquela, 1967, which may be more primitive. Finally, as Paul noted in his text (p. 512), the astragalus is not reduced in primitive ornithischians, and this character is most parsimoniously considered convergent; it is therefore unclear why it is considered a synapomorphy on the cladogram.

The apomorphies posited by Paul as allying Prosauropoda with Ornithischia and Segnosauria are similarly facile. Both hypotheses do not hold up in light of the characters placing Prosauropoda within Saurischia and Sauropodomorpha (Gauthier, 1986), and Therizinosauroidea within Saurischia and Theropoda.

Some other characters discussed by Paul deserve comment. Contrary to statements in his paper, there is no evidence for a diastema within the tooth row of *Erlicosaurus andrewsi,* the pubic peduncle of the therizinosauroid ilium does not project anteriorly as in ornithischians (cf. his fig. 4), and his interpretation of the posterior part of the maxilla and the ectopterygoid on the palate is inaccurate (apparently based on fig. 6 of Perle [1981]). Paul considered the occiput to be "low," but he was apparently misled by the forward slope of the dorsal part of the occiput, which fore-

shortens the occiput in posterior view (cf. fig. 2 of Perle [1981]).

The presence of cheeks is the only feature shared unequivocally by Therizinosauroidea and Ornithischia and lacking in Theropoda. Considering all of the evidence, this is most parsimoniously considered to be convergence.

THE SAUROPODOMORPH HYPOTHESIS

Sauropodomorph affinities for therizinosauroids were hypothesized by Gauthier (1986), but no character evidence was adduced. Of the four characters used by Gauthier to diagnose Sauropodomorpha (p. 45), only "lanceolate teeth with coarsely serrated crowns" may apply to this group.

In a brief abstract, Sereno (1989) suggested that therizinosaurids are the sister group of a monophyletic Prosauropoda, and he supported this with six characters: "1) a beak, 2) ventrally curved dentary tip, 3) inset first dentary tooth, 4) L-shaped premaxilla-maxilla suture, 5) horizontal premaxillary posterior process, and 6) secondary antorbital fossa wall." The short descriptions make evaluation of these characters difficult, but it appears that characters 1–5 are also present in ornithomimosaurs, and for at least 1 and 2, the condition in ornithomimosaurs and segnosaurs is much more similar than the condition in prosauropods. The description of character 6 is ambiguous but may refer to the well-developed rim around the fossa, which is indeed similar in prosauropods and *Erlicosaurus andrewsi*.

Considering the cranial evidence, the hypothesis of a close relationship between Therizinosauridae and Prosauropoda (or Sauropodomorpha as a whole) is supported only by a vague resemblance of the cheek teeth and by the presence of a well-developed rim around the antorbital fossa.

AUTAPOMORPHIES OF *ERLICOSAURUS ANDREWSI*

The skull of *Erlicosaurus andrewsi* possesses several peculiarities, some of which are unique among dinosaurs. Unfortunately, because the skulls of other Therizinosauroidea are unknown, it is not possible to determine how broadly these characters are distributed among its members.

The premaxilla is edentulous in several taxa of Theropoda, including all extant avians, but the precise structure exhibited by *Erlicosaurus andrewsi* (figs. 1–4) is to our knowledge unique. The nearly vertical labial margin terminates in a sharp edge forming a broad U shape in ventral view that extends well below the level of the palate. This structure is much less robust than the premaxilla of Oviraptorosauria and lacks the denticles of the latter; it is more similar to that of Ornithomimosauria. The premaxilla of ornithomimosaurians, however, does not extend ventrally much beyond the level of the palate.

The nares of *Erlicosaurus andrewsi* are unusually large due to the anterior brevity of the maxilla (figs. 1–3). No nonavian theropod has nares this large. Unlike nonavian Theropoda (except troodontids), the premaxilla does not extend posterodorsally along the maxilla to form the posterior border of the nares; as noted above, this is likely due to the large size of the nares.

The antorbital fossa of *Erlicosaurus andrewsi* is bordered by a well-developed, thin rim (figs. 1, 2, 5). This rim is similar to that of the basal saurischians *Eoraptor lunensis* and *Plateosaurus engelhardti*, but is more pronounced.

The medial wall of the antorbital fossa of *Erlicosaurus andrewsi* apparently lacks an accessory antorbital fenestra (figs. 1, 2, 5). Further preparation may reveal a small fenestra near the ventral or anterior border of the fossa, but it would be unusually small and in a strange position. An accessory fenestra is present in all nonavian Theropoda where this feature can be determined.

The maxilla of *Erlicosaurus andrewsi* has a dentition that is inset from the labial margin (figs. 1, 2, 4), and its lateral surface has few nutrient foramina posteriorly, except for a large, anteriorly opening foramen (figs. 1, 2, 5). Together these features, unknown in other Theropoda, suggest the presence of cheeks, such as are inferred to have been present in Ornithischia (Galton, 1973).

The jugal of *Erlicosaurus andrewsi* extends much further posterodorsally than in other Theropoda, ascending the quadratojugal to form much of the posterior border of the low-

er temporal fenestra (fig. 1). In some Ornithomimosauria the jugal ascends the quadratojugal (Osmólska et al., 1972), but this is due to the displacement of the quadratojugal anteriorly to meet the postorbital bar.

The vomer of *Erlicosaurus andrewsi* is much longer than that of any other dinosaur of which we are aware (fig. 4). Although the vomers of the primitive ornithischian *Lesothosaurus diagnosticus* and, to a lesser extent, the theropod *Allosaurus fragilis,* are elongate, they are shorter than in *Erlicosaurus andrewsi*. In *Erlicosaurus andrewsi* the vomer continues posteriorly to articulate around the unusually short cultriform process (fig. 6), rather than with the pterygoid, another highly unusual condition.

The parabasisphenoid is pneumatic in birds and several groups of theropods, but never to the extent present in *Erlicosaurus andrewsi* (fig. 8). Among primitive theropods this condition is most closely approached by ornithomimids and troodontids, but the parabasisphenoid cavity of *Erlicosaurus andrewsi* appears to be at least twice as large as in these taxa. The pneumatic cavities are remarkably similar to those of protosuchid crocodyliforms (Busbey and Gow, 1984).

The greatly expanded braincase has modified the passage for the internal carotid artery, as well as the external auditory meatus (fig. 7). The passage for the internal carotid artery continues posteriorly all the way to the occiput, unlike in other nonavian theropods where there is no evidence of this artery posterior to where it enters the braincase anterior to the ear. Furthermore, the braincase greatly constricts the ventral part of the external auditory meatus. In other nonavian theropods, the passage for the internal carotid artery is not enclosed on the occiput, and the quadrate is broadly separated from the braincase such that a distinct external auditory meatus is not formed.

The exit for the trigeminal nerve on the side wall of the braincase of *Erlicosaurus andrewsi* is unusual in having passages for each of the nerve's three branches. In archosaurs primitively there is but a single opening, and in carnosaurian and troodontid theropods there are two (Currie and Zhao, 1993).

The teeth of *Erlicosaurus andrewsi* (fig. 12) and other Therizinosauroidea are unusual among theropods, although not entirely unique. Their subcircular basal cross section, lacking the mediolateral compression typical of theropod teeth, is similar to the plesiomorphic condition in the theropod sister group, Sauropodomorpha, and to the anterior upper teeth of the most primitive theropod, *Eoraptor lunensis* (Sereno et al., 1993). The lanceolate form of the maxillary teeth and posterior dentary teeth is also mirrored in the teeth of these two taxa. In no other theropods, however, is the dentition composed nearly exclusively of such teeth. The coarseness of the serrations on the "cheek" teeth of *Erlicosaurus andrewsi* and other therizinosauroidea is matched only on the teeth of most Troodontidae (Farlow et al., 1991), but troodontid teeth are sharply recurved.

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